BREEDING ECOLOGY OF NORTHERN PINTAILS: NESTING ECOLOGY, NEST-SITE SELECTION, NUTRIENT RESERVE USE AND BROOD ECOLOGY

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ABSTRACT

To better understand the life-history of Northern Pintails (*Anas acuta)*, and the evolutionary forces that may have shaped it, I examined constraints and consequences of breeding-season decisions. General patterns and trade-offs over time and energy use were evaluated for nutrient reserve allocation to egg formation, nest-site selection, nesting effort and raising offspring.

To meet nutritional demands of egg laying, female pintails obtain nutrients from either exogenous or endogenous sources. I examined use of nutrient reserves during egg formation in pintails and tested whether reserves regulated clutch size. I found that females relied heavily on fat reserves during egg laying, but found no evidence that fat, or protein, proximately limited clutch size.

Birds typically do not distribute their nests randomly among habitats, and it is generally assumed that non-random nest placement results from natural selection. I tested whether nest-site selection patterns were based on vegetative features, female characteristics, or whether site selection was based on nest microclimate. Relative to random sites, pintail nests had less short grass, more shrub cover, and were more frequently found in depressions; unsuccessful nests were closer to shrubs than were successful ones. The microclimate of nests differed from that of random sites, nests being about 2° C cooler on average than random sites during daylight hours. Furthermore, 30-minute mean temperatures exceeded the upper lethal limit for embryonic development more often at random sites than at nest- sites. Overall, pintails exhibited nest-site selection based principally on vegetation and microclimatic conditions, the latter perhaps to benefit developing embryos.

The amount of time and energy that individuals allocate to reproduction has presumably evolved in response to diverse selective pressures. I evaluated variation in nesting effort and success of female pintails breeding in prairie habitats. I found no relationship between egg size and clutch size, or evidence from one year to the next of a trade-off between current and future investment in eggs. However, greater investment in initial clutches led to longer delays in laying replacement clutches the same year. Therefore, because delays in renesting are costly (late-nesting females produce fewer offspring), females must contend with a tradeoff between maximizing reproductive output in initial clutches versus risk of delayed renesting.

Implicit in many studies is the assumption that nesting success is an appropriate measure of reproductive success, but recent evidence reveals much variation in post-hatch survival of ducklings. I examined brood and duckling survival from radio-marked females and related duckling survival to maternal and environmental attributes. Duckling survival ranged from 42-65% with most duckling mortality occurring during the first 10 days post-hatch. Ducklings in relatively small broods had higher survival than ducklings from larger broods in 2 of 3 years, suggesting a further constraint on clutch size. Thus, trade-offs occurring at several stages likely set limits to clutch size in pintails, illustrating the need for a more comprehensive template in future studies of clutch size determinants in waterfowl and other species.

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Man, like a barefoot boy draining rain puddles with his big toe, has systematically emptied the marshes of our prairies with ditch and drain pipe. Such conquest has been complete. An eagle still rides the wind above the mountain, but where the fens are gone the wild duck comes no more. A patch of nettles, parched, cracked earth, a swirl of dust on a summer day – that is the vanquished marsh.

H. Albert Hochbaum

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CHAPTER 1. GENERAL INTRODUCTION

Observed life-histories of plants and animals are characterized by enormous variability, creating rich opportunity for investigation of these patterns. A species' life-history can be perceived as the sum of a series of choices made by individuals, with each of these choices influencing survival or lifetime reproductive success, and hence, fitness. Since choices typically occur sequentially, rather than concurrently, early choices can constrain subsequent ones. For example, the choice of breeding habitat will determine the range of nesting sites available, the potential predation risk and the physical environment. To understand the life-history of an organism and the evolutionary forces that have shaped it, I wanted to understand the constraints under which decisions are made and the consequence of those decisions (Beletsky and Orians 1996). Therefore, this thesis is organized around a sequence of breeding-season decisions made by Northern Pintails (*Anas acuta*) in southern Alberta. For several reasons, I concentrated on major decisions relating to nutrient reserve allocation to egg formation, nest-site selection, nesting effort, and brood rearing.

Life-history traits of pintails are unique among upland nesting ducks. Pintails are among the earliest nesting duck species (Bellrose 1980), have one of the smallest clutch sizes (Austin and Miller 1995), and typically breed in challenging environments characterized by wide fluctuations in climate, and timing and duration

of resource availability during the nesting and brood rearing periods. Furthermore, pintails are unique among North American waterfowl in that many nest in prairie and arctic habitats (Calverly and Boag 1977), creating a novel opportunity to look at intraspecific geographic variation in reproductive strategies. Consequently, these distinct ecological features and traits create a unique template for exploring reproductive trade-offs in birds.

Many species of northern temperate birds must breed, nest, and raise their young during a relatively short summer. In addition to season length constraints, environmental factors often vary temporally and can exert strong constraints on reproductive effort and success. For example, nutritional requirements of egg laying are often hypothesized to limit egg production (i.e., egg-production hypothesis; Ankney et al. 1991) but, alternatively, factors related to timing of nesting (such as seasonal declines in food availability or recruitment potential of young) may cause females to exercise restraint when forming eggs.

I first focus on use of nutrient reserves for egg formation in pintails (Chapter 2), and compare these patterns with those for pintails nesting in Alaska. During clutch formation, female waterfowl commit relatively large amounts of fat, protein and mineral to egg development (Sotherland and Rahn 1987). To meet these nutritional demands, females obtain nutrients from either exogenous or endogenous sources, the level of reliance varying among waterfowl species. Until recently, hypotheses regarding clutch size limitation focused primarily on egg production costs, without considering costs during incubation and thereafter. Factors other than nutrient reserves and exogenous nutrients might limit clutch size. In Chapter 2, I examine

use of nutrient reserves during egg formation in Northern Pintails, ask whether reserves regulate clutch size and examine if pintails withhold some nutrients for later use.

I then look at nest-site selection in pintails, in terms of vegetative, microclimatic features and characteristics of females, to elucidate patterns and consequences of site selection with respect to clutch survival (Chapter 3). Ground-nesting grassland birds usually suffer high rates of predation (Martin 1988, 1993, Beauchamp et al. 1996); therefore, tactics or traits that help nesting birds avoid predation should be favored (With 1994), particularly those that are learned rapidly or inherited (Endler 1986). Therefore, in Chapter 3, I evaluate nest-site selection in Northern Pintails, and determine whether patterns, if they exist, are consistent with site-selective predation on nests (Clark and Shutler 1999).

Amelioration of nest microclimate may also be an important consideration in nest-site choices by birds (e.g., Walsberg 1985), but putative thermal advantages of nest-site selection are rarely measured directly (e.g., Peterson and Best 1985, Beckoff et al. 1987, Sakai and Noon 1991, Gloutney and Clark 1997). By selecting microclimates that reduce costs, birds may reduce energy requirements or reallocate conserved time or energy to other activities (Walsberg 1985, 1986, Webb and Rogers 1988) or future offspring (Kilpi and Lindstrom 1997). However, evidence for microclimate selection by nesting ducks is generally lacking and equivocal (Gloutney and Clark 1997), so further work is needed to more fully test this possibility. Therefore, in Chapter 3, I also characterize the microclimate at pintail

nest-sites and determine if nest-site selection was based on microclimatic differences.

Understanding how energy allocation strategies influence life-history decisions and trade-offs has been difficult (Stearns 1989, 1992). It is also important to distinguish between energetic costs of breeding and reproductive costs (Clutton-Brock 1984). For instance, energy and nutrients invested in egg production varies with the size, quality, and number of eggs, but reproductive costs include maintaining adequate energetic reserves to ensure successful hatching and adult survival after egg production (Martin 1987a). Pintails lay small clutches relative to other dabbling ducks (Austin and Miller 1995), suggesting that they may withhold nutrients for other activities (e.g., renesting, incubation). For example, the laying of additional eggs may reduce opportunities for renesting due to either energetic or time constraints. Thus, in Chapter 4, I examine whether there is a trade-off between the size of initial clutches and the amount of time required to produce a replacement clutch. Egg size is also an important determinant of reproductive investment; therefore adjustments in energetic investment may be reflected in egg size and/or clutch volume. In most species of waterfowl, individual females show a high repeatability for egg size, suggesting that they cannot alter egg size in response to environmental conditions (Flint and Sedinger 1992). I assessed variation in clutch volume while examining current versus future investment in eggs. Because reproductive success of upland ducks is strongly dependent on nest success and renesting effort, in Chapter 4 I look at variation in nesting effort and success of female pintails breeding in a prairie habitat.

Considerable attention has focused on nesting success of ducks, but much less is known about processes affecting brood-rearing and recruitment (Johnson et al. 1992, Rotella and Ratti 1992a). Implicit in many studies is the assumption that nesting success is an appropriate measure of reproductive success (Greenwood et al. 1987), but recent evidence reveals much variation in post-hatch survival of ducks (see Grand and Flint 1996b for review). Thus, further work is needed to evaluate sources of variation in duckling survival and to more adequately assess individual reproductive performance. In Chapter 5, I address this deficiency by looking at brood-rearing success of individually marked female Northern Pintails, and relate duckling survival to maternal and environmental attributes.

To achieve many of my objectives, I needed to capture female pintails early in the spring, and individually mark them with colored nasal discs and radio transmitters. Decoy traps have been widely used to trap waterfowl in the spring (Anderson et al. 1980, Sharp and Lokemoen 1987, Dwyer and Baldassarre 1994), but trap bias has rarely been examined. Radio telemetry is also frequently utilized in waterfowl research (e.g., Ball et al. 1975, Cowardin et al. 1985, Grand and Flint 1996b, Cox and Afton 1997), and transmitters can have negative effects on waterfowl (Sorenson 1989, Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997). Researchers who attempt to evaluate transmitter or marker effects often ignore the possibility that observed effects may result from a combination of trapping and marking. Therefore in Appendix 1, I quantify possible trap bias, and combined effects of capture, nasal-marking and radio-marking, on reproduction of female pintails.

Although much of my research was designed to evaluate specific ecological questions, I do not wish to lose sight of its relevance to applied problems. Pintail populations have dramatically declined in the last two decades, and they do not appear to be recovering. Since 1955, when the U.S. Fish and Wildlife Service (USFWS) and Canadian Wildlife Service (CWS) began surveys of waterfowl populations and spring ponds, until the late 1970s, Northern Pintail populations in prairie Canada tracked the abundance of spring ponds. Declines in both pintails and ponds were evident through the drought of the 1980s; however, with the return of abundant water to the prairies in the early to mid 1990s, pintails failed to rebound as did several other duck species. In 2000, pintail populations remained 33% below the long-term average. In contrast, all other dabbling ducks ranged from 3% to 100% above their long-term averages (Wilkins et al. 2000). The prolonged decline and lack of recovery in pintail populations has sparked much concern within conservation organizations. There is much yet to be done, for pintails and other species that share the prairies.

CHAPTER 2. NUTRIENT RESERVE DYNAMICS OF NORTHERN PINTAILS BREEDING IN ALBERTA

2.1 Introduction

During clutch formation female waterfowl commit relatively large amounts of fat, protein and mineral to egg development (Sotherland and Rahn 1987). To meet these nutritional demands, females obtain nutrients from either exogenous or endogenous sources, the level of reliance varying among waterfowl species (Alisauskas and Ankney 1992). For instance, some arctic nesting eiders (*Somateria mollissima*) rely almost completely on endogenous reserves for clutch formation (Parker and Holm 1990). Tactics utilized by Anatini and Aythyini are less clear (Krapu and Reinecke 1992), although it is generally recognized that endogenous reserves are an important source of nutrients (Alisauskas and Ankney 1992). For example, in most species studied, fat reserves are utilized to varying degrees (Ankney and Alisauskas 1991a). Protein reserves are often utilized in species with primarily herbivorous diets (e.g. Gadwall; [*Anas strepera*]), whereas mineral reserves are generally not used (Ankney and Alisauskas 1991b). However, the degree to which nutrient reserves regulate clutch size is debated (Ankney et al. 1991, Arnold and Rohwer 1991).

Until recently, hypotheses regarding clutch size limitation focused primarily on egg production costs, without considering costs during incubation and thereafter. Factors other than nutrient reserves and exogenous nutrients may limit clutch size. For

example, restraint in use of nutrient reserves would be favoured if females with greater nutrient reserves after laying experience higher reproductive success (Ankney and Alisauskas 1991b). This hypothesis predicts that withholding some nutrients that would otherwise be committed to egg production could be used to offset costs associated with post-laying activities, such as incubation and brood rearing (see Blums et al. 1997b for a brief review). Here, I examine use of nutrient reserves during egg formation in northern pintails (*Anas acuta;* hereafter pintails), ask whether reserves regulate clutch size and examine if pintails withhold some nutrients for later use.

Nutrient dynamics of pintails are particularly interesting because they nest early in the season relative to other North American ducks (Bellrose 1980, Austin and Miller 1995) and may therefore be more dependent on endogenous reserves to meet nutritional requirements of egg formation. In addition, pintails lay small clutches relative to other dabbling ducks (Austin and Miller 1995) suggesting that they may withhold nutrients for other activities (e.g., renesting, incubation). To investigate this, I conducted an interspecific comparison of dabbling ducks nutrient reserve use based on published literature. Furthermore, pintails are unique among North American waterfowl in that many nest in prairie and arctic habitats (Calverly and Boag 1977), creating a novel opportunity to look at intraspecific geographic variation in use of endogenous reserves by egg-laying females. Two recent studies evaluated nutrient reserve dynamics of pintails in Alaska (Mann and Sedinger 1993, Esler and Grand 1994b), but there are no comparable data from the prairies. Therefore, my objectives were to study seasonal fat and protein dynamics of prairie-nesting pintails, and assess the role of stored reserves in clutch size regulation.

2.2 Methods

2.2.1 Study Area and Methods

Work was conducted on wetland complexes located within a 35 km radius of Brooks, Alberta (50° 33' N, 111° 55' W). The area surrounding these wetland complexes is dominated by mixed grass prairie and is subject to seasonal grazing by cattle. See Chapter 3 for more detail.

Eighty-one female pintails were collected (under permit from Canadian Wildlife Service) from arrival through incubation in 1992, 1993 and 1996; females were shot from concealed locations or by pass shooting. Due to logistical constraints, the majority of early season birds were collected in 1992 and no birds were collected after 2 June (Table 2.1). Because few incubating females were collected (n = 2), they were excluded from the sample.

On the day of collection, all birds were weighed (nearest 10 g, with a Pesola scale) and I then removed the ovary, oviduct and oviducal egg if present. In 1992 and 1993, reproductive tissue was placed in 10% formalin after assessing reproductive state. In 1996, the number and weight of developing follicles, the number of postovulatory follicles, ovary and oviduct weight, and presence or absence of an oviducal egg were recorded, but the reproductive tract was not preserved. Carcasses were then labeled, sealed in plastic bags, and frozen.

In the laboratory, specimens were thawed and two measurements were taken with dial calipers: tarsus length (nearest 0.1 mm) - from distal point of foot bent toward body, to notch at ankle, and culmen (0.1 mm) - distance from anterior tip of bill to

Table 2.1. Collection dates for Northern Pintails in each reproductive category in 1992, 1993 and 1996, near Brooks, Alberta.

Reproductive Category	1992	1993	1996
Pre- RFG	25 March – 18 April	24 - 26 April	-
	(26)[a]	(1)	
RFG	7 - 12 April	20 - 29 April	24 April - 1 May
	(4)	(8)	(5)
Laying	24 April - 2 June	21 - 27 April	23 April - 2 May
	(9)	(11)	(15)

[a]sample size. In 1992, two birds collected in June and classified as pre-RFG were deleted from the sample.

feather line. Wing chord (0.1 mm) - distance from wrist of bent wing to most distal point of primary feathers was measured with a flat ruler. Two internal measurements were taken (with calipers) after removal of skin and feathers,: keel (0.1 mm) - distance along median line from anterior notch to posterior point of sternum, and spine length (0.1 mm) - from joint behind last cervical vertebra to joint anterior to first mobile caudal vertebra.

Breeding status was assigned based on characteristics of the reproductive tract. Birds with no developing follicles (minimum diameter of 8 mm) and no post-ovulatory follicles were classed as "pre-rapid follicle growth" (pre-RFG). Birds with yolky developing follicles, no post-ovulatory follicles and no oviducal egg were classed as "rapid follicle growth" (RFG). Birds with an oviducal egg, and post-ovulatory follicles, were classed as "layers". Birds with no oviducal egg, no developing follicles but with post-ovulatory follicles, were classed as "post-laying".

2.2.2 Carcass Analysis

Birds were plucked and digestive tract contents were removed. The right breast muscles and leg muscles (Ankney and MacInnes 1978) were removed and weighed wet (0.01 g; with Ohaus balance). The heart, gizzard, oviduct (in 1992 and 1993), and liver were removed and weighed wet. The breast and leg muscle, heart, gizzard, and liver were then oven-dried separately to constant weight at approximately 90° C. In 1992, a piece of heart tissue was removed for genetics work before drying. Dry mass of this removed heart tissue was determined by extrapolating from the percent water in the remaining piece of heart. Abdominal fat deposits were removed, weighed and discarded. Nutrient contents of muscles of the right breast and leg, liver and the

remaining carcass were determined using petroleum ether in a modified Soxhlet apparatus (Dobush et al. 1985) and ashing in a muffle furnace to determine proportions of protein and mineral (Ankney and Afton 1988).

Total nutrient reserve levels (Fat, Protein, and Ash) were determined using techniques described by Ankney and Afton (1988). From these determinations, I calculated nutrient reserve levels for each bird. For example, total Fat:

$$\text{Fat} = F_{\text{carcass}} + F_{\text{abdomen}} + F_{\text{leg}} + F_{\text{breast}} + F_{\text{liver}}, \quad (2.1)$$

and total Protein:

$$\text{Protein} = L_{\text{carcass}} + L_{\text{leg}} + L_{\text{liver}} + L_{\text{breast}} - \text{Ash}, \quad (2.2)$$

where L is lean dry mass and F is fat in each body component.

2.2.3 Reproductive Tissue Analysis

Measures of both nutrient reserves and reproductive nutrients (nutrients committed to oviduct, ovary, oviducal egg and eggs laid) are required for analyses of nutrient reserve dynamics. The following procedures were used in 1992 and 1993. The ovary (which included all developing follicles and post-ovulatory follicles) was treated like the leg and liver. The oviduct was dried and weighed: the resulting dry mass was considered protein.

Completely developed oviducal eggs were analyzed for fat and protein content. Nutrients in eggs already laid were estimated by multiplying the number of eggs laid (based on the number of postovulatory follicles) by estimates of fat and protein in each egg. Estimates of egg fat and protein in each egg were determined either by (1) the amount of those nutrients in the female's completely developed oviducal egg, if present;

or (2) the average amount of nutrients in pintail eggs from a sample of oviducal eggs. The former was used when possible. Ten completely formed oviducal eggs were used to determine average nutrient content of pintail eggs. Oviducal eggs were separated into hard shell (if evident), albumen, and yolk and dried to constant weight. The entire dry yolk was extracted to determine fat content. Due to few complete eggshells in my sample, I used an average of 3.00 g for mass of egg shell as reported by Esler and Grand (1994b). Average lipid and protein in pintail eggs was 4.18 g and 6.29 g.

Fat invested in clutch formation (R-Fat) was estimated following

$$\text{R-Fat} = F_{\text{ovary}} + F_{\text{yolk fat}}(N_{\text{POF}}) \qquad (2.3)$$

where F_{ovary} was fat in the ovary (including all follicles), N_{POF} was number of ovulated follicles, and $F_{\text{yolk fat}}$ was yolk fat.

Protein associated with clutch formation (R-Protein) was estimated as

$$\text{R- Protein} = L_{\text{ovary}} + L_{\text{oviduct}} + N_{\text{POF}}(L_{\text{yolk}} + L_{\text{albumen}}) \qquad (2.4)$$

where L_{ovary} and L_{oviduct} were the lean dry mass of the ovary (including all follicles) and oviduct for each female, and $L_{\text{yolk}} + L_{\text{albumen}}$ were the average lean dry fractions of yolk and albumen per egg.

Minerals in the clutch, R-Ash, were estimated as

$$\text{R-Ash} = N_{\text{POF}}(\text{Megg}) \qquad (2.5)$$

where M_{egg} is mean mass of eggshell.

In 1996, the reproductive tracts were utilized for an isotope study and were not available for analysis. Therefore, to estimate R-Fat and R-Protein I used simple linear regressions (using data from D. Esler, n = 152 female pintails) to determine the relationship between ovary wet weight and ovary fat, oviduct wet weight and oviduct dry weight and ovary wet weight and ovary protein. Ovary includes ovary tissue and all developing and post-ovulatory follicles. The following equations were obtained

$$\text{Ovary Fat} = -0.4305 + 0.2678(\text{ovary wet weight}); \quad (2.6)$$

$$R^2 = 0.96 \; P = 0.0001,$$

$$\text{Oviduct Dry Weight} = 0.2376 + 0.1994\,(\text{oviduct wet weight}); \quad (2.7)$$

$$R^2 = 0.94, \; P = 0.0001,$$

$$\text{Ovary Protein} = -0.2436 + 0.2621\,(\text{ovary wet weight}); \quad (2.8)$$

$$R^2 = 0.96, \; P = 0.0001.$$

R-Fat, R-Protein and R-Ash were then calculated following methodologies outlined above for 1992 and 1993.

2.2.4 Statistical Analysis

I assessed body size (Ankney and Afton 1988) by conducting principal components analysis (PROC PRINCOMP; SAS 1996) on the correlation matrix of the following five variables: wing chord, tarsus length, culmen length, spine length and keel length. The resulting first principal component described positive correlations among variables with loadings ranging from 0.42 to 0.47, had an eigenvalue of 2.42, and explained 48.5% of the total original variance. I used scores from the first principal component (PC_1) as an indicator of body size and regressed nutrient reserves against PC_1.

I used *t*-tests ($P < 0.05$) to determine if organ size, nutrient reserves and nutrients committed to reproduction differed between temporally adjacent breeding categories (i.e., Pre-RFG, RFG and Laying). For direct comparison to previous studies, I used simple linear regressions to describe relationships between nutrient reserves and reproductive nutrients (Alisauskas and Ankney 1992). To examine additional variation in each nutrient reserve, Analysis of Covariance (ANCOVA, PROC GLM) was used with year as a main effect and reproductive investment and date of collection as covariates.

If nutrient reserves limit clutch size, and there is a minimum threshold that determines the end of egg laying, then females with different clutch size phenotypes will lie on different trajectories of nutrient reserves versus reproductive investment (Sedinger et al. 1997). To assess the role of nutrient reserves in limiting clutch size, I used ANCOVA with final clutch size and year as fixed factors and investment in reproduction and collection date as covariates (Sedinger et al. 1997). To estimate final clutch size, I restricted the analysis to females that had laid ≥ 3 eggs (i.e., at least 3 post-ovulatory follicles) and used the number of rapidly developing follicles to estimate the number of eggs yet to be laid (Ankney and Afton 1988). Restricting the sample to females that had laid at least three eggs seemed reasonable, since the maximum number of developing follicles that can be consistently detected in pintails is 4 (Esler 1994) and mean clutch size in southern Alberta is 7 (Guyn and Clark 2000).

To examine if pintails withhold nutrients (i.e, fat) for post-laying activities, I examined the relationship between fat reserves (corrected for lean body mass) at the end of laying and the amount of fat committed to egg production (fat/egg x clutch size;

corrected for lean body mass) for seven upland nesting duck species. I used lean body mass (based on late incubation masses) of 311, 469, 560, 612, 639, and 811 for blue-winged teal (*Anas discors*), northern shoveler (*Anas clypeata*), American wigeon (*Anas americana*), northern pintail, gadwall and mallard (*Anas platyrhynchos)* (R. G. Clark unpubl. data, Duncan 1987a, Forbes et al. 1994). I used clutch sizes (first nests) of 10, 10, 9, 8, 10, and 9 for blue-winged teal, northern shoveler, American wigeon, northern pintail, gadwall and mallard, respectively (Duebbert 1966, DuBowy 1996, Lack 1968, Devries unpubl. data, K. L. Guyn unpubl. data, R. G. Clark unpubl. data). I assumed lean body mass and clutch size for cinnamon teal (*Anas cyanoptera*) was the same as estimates for blue-winged teal. The size of fat reserves at the end of laying was determined by using equations reported in the literature for the relationship between fat reserves and reproductive fat for the seven species (Krapu 1981, Ankney and Afton 1988, Ankney and Alisauskas 1991b, Alisauskas and Ankney 1992, Gammonley 1995, Mann and Sedinger 1993, Young 1993, Esler and Grand 1994b, Guyn and Clark, this paper). Fat committed to reproduction was estimated by multiplying clutch size by the amount of fat per egg. I used linear regression (PROC REG) to determine the relationship between fat reserves at the end of laying and fat committed to egg production and then examined where pintails fell relative to the regression line. I also checked for non-linear relationships.

Initial statistical models included all main effects listed, plus all two-way interactions. I determined statistical significance of individual effects based on type III sums of squares. I deleted nonsignificant ($P > 0.05$) effects, beginning with the highest P value, until all remaining variables were either significant or included within a

significant interaction, provided that the overall model also was significant at $P < 0.05$. All significance tests were two-tailed at $\alpha = 0.05$. Retrospective power analysis was determined using SAS programming language. Means and least-squared means are presented ± SE.

2.3 Results

2.3.1 General Breeding Chronology

General breeding chronology is not known for 1992 or 1993. However, median arrival date of pintails in southern Alberta during 1994 - 1996 was 18 March, with the earliest nest initiations ranging from 7 - 18 April and the latest initiations occurring from 17 - 21 June (n = 293, Guyn and Clark 2000).

2.3.2 Muscle and Organ Dynamics

I excluded two females from the pre-RFG category. Although classified as pre-RFG, they were collected in early June, 44 days later than other pre-RFG females. Gizzard muscle mass was at a maximum during pre-RFG, decreased 10 g between pre-RFG and RFG and lost an additional 3 g between RFG and laying (Table 2.2). Breast muscle mass was nearly 7 g heavier during RFG than during pre-RFG. Liver mass increased from pre-RFG to RFG, but did not change between RFG and laying. Leg muscle mass and ceca length did not differ between reproductive categories.

2.3.3 Nutrient Reserve Dynamics

Fat reserves and ash did not vary by year ($P > 0.2$), but protein reserves were lower ($F = 14.2$, $P < 0.001$) in 1992 (least square means; 1992, 127.5 ● 1.1 g; 1993, 134.8 ±

Table 2.2. Organ size (g, except ceca length is in mm; mean ± SE) for female Northern Pintails during the breeding season, near Brooks, Alberta.

Variable	Pre-RFG		RFG		Laying
Gizzard	28.8 ± 0.8	***[a]	18.8 ± 1.1	•	15.5 ± 0.7
Liver	13.8 ± 0.6	*	15.7 ± 0.8	ns	16.6 ± 0.5
Right Breast Muscle	75.3 ± 1.4	***	82.1 ± 1.8	ns	79.7 ± 1.2
Right Leg Muscle	22.4 ± 0.5	ns	22.5 ± 0.6	ns	21.8 ± 0.4
Ceca Length	225 ± 8	ns	199 ± 10	ns	202 ± 7

[a] significance level of comparisons between adjacent columns: ns indicates $P > 0.05$; *, $P = 0.05$, **, $P = 0.01$, *** $P = 0.001$; with *t*-tests.

1.6 g; 1996, 136.8 ±1.6 g). Therefore, for this analysis, protein reserves were corrected for year effects. Nutrient reserves did not vary between reproductive categories, except for a decrease in fat and body mass between RFG and laying, and an increase in protein reserves between pre-RFG and RFG (Table 2.3). Females were heaviest, having most fat, during pre-RFG.

Fat reserves were not related to body size ($P = 0.18$), but relationships were found with protein and mineral ($P < 0.001$). I did not detect any non-linear relationships between nutrient reserves and PC_1 ($P > 0.2$). Residuals from these models were used to generate new protein and mineral values corrected for body size (see Ankney and Alisauskas 1991b); corrected values were used in all analyses.

Fat reserves of females declined significantly ($P = 0.001$, $R^2 = 0.33$) through egg laying as indicated by

$$Y = 108.5 - 2.44X, \qquad (2.9)$$

where Y = fat reserves and X = reproductive fat. Regression of size corrected protein reserves on reproductive protein indicated no statistical relationship between the two variables ($P = 0.18$). The equation was,

$$Y = 130.2 + 0.07X, \qquad (2.10)$$

where Y = protein reserves and X = reproductive protein. Regression of ash (mineral reserves) on reproductive ash also indicated no statistical relationship between the two variables ($P = 0.16$). The equation was,

$$Y = 25.3 + 0.04X, \qquad (2.11)$$

where Y = ash and X = reproductive ash.

Table 2.3. Nutrient reserves and body mass (g) of female Northern Pintails during the breeding season near Brooks, Alberta. Where appropriate, data are least-squared means (x ± SE) controlling for body size (PC1) and annual variation.

Variable	Pre-RFG		RFG		Laying
Body Composition					
Body Mass	783 ± 13	ns[a]	772 ± 17	*	723 ± 13
Fat	119.8 ± 8.8	ns	103.2 ± 8.7	***	61.0 ± 4.1
Protein	127.8 ± 1.6	*	133.1 ± 1.9	ns	133.0 ± 1.3
Ash	24.4 ± 0.4	ns	25.5 ± 0.4	ns	26.4 ± 0.3

[a] significance level of comparisons between adjacent columns: ns indicates P > 0.05; *, P = 0.05, **, P = 0.01, ***, P = 0.001; with t-tests.

General linear models (Table 2.4) better explained the variation in the data. In pre-RFG females, fat, protein and ash reserves did not vary with date or year. However, only one pre-RFG female was collected after 1992. Laying females (RFG and laying) in 1993 lost body fat at a higher rate (Figure 2.1) than in 1992 and 1996. Protein and ash reserves were unaffected by investment in clutch formation. Fat and ash reserves declined with collection date, 1.7 g and 0.05 g per day respectively; but protein reserves did not vary with collection date. Protein and ash reserves varied by year; females collected in 1993 and 1996 averaged 10 g more protein and 2 g more ash than those from 1992.

For 21 females collected with at least 3 post-ovulatory follicles, I estimated final clutch size based on the number of rapidly developing follicles (range; 0-4 rapidly developing follicles). To test if clutch size was regulated by nutrient reserves, I examined whether final clutch size was related to nutrient reserves with investment in reproduction as a covariate (Table 2.5). Protein and ash reserves were unrelated to reproductive nutrient investment or final clutch size. Fat reserves tended to vary by year, but were also unrelated to reproductive investment or final clutch size. Due to small effect and sample sizes, power of these tests was low ($P < 0.35$).

I used data for seven species from 11 studies to examine the relationship between the amount of fat reserve left at the end of laying (corrected for body size) and the amount of fat committed to egg laying (also corrected for body size). Species that had the largest fat reserves left at the end of laying tended to have the largest clutch sizes ($F = 16.99$, df = 1,10, $P = 0.002$). This result held when the analysis was conducted with mean egg weight instead of lipid weight per egg ($F = 9.4$, df = 1, 10, P

Table 2.4 Nutrient reserves of pre-RFG and laying (includes RFG and laying) female Northern Pintails in relation to year (1992, 1993, 1996), collection date, and nutrient commitment to clutch formation (R-Nutrient; assessed for layers only). Only significant effects are presented.

Dependent Variable	Model			Independent variable		
	F	P	R^2		F	P
Pre-RFG						
Fat	0.02	0.98	0.002			
Protein	0.73	0.49	0.06			
Ash	0.22	0.64	0.01			
Layers						
Fat	12.5	0.0001	0.63	Date	28.4	0.0001
				Year	3.8	0.03
				R-Fat	8.9	0.005
				R-Fat • Year	4.7	0.01
Protein	4.56	0.004	0.28	Year	7.8	0.001
Ash	2.2	0.08	0.16	Date	5.7	0.02
				Year	3.1	0.06

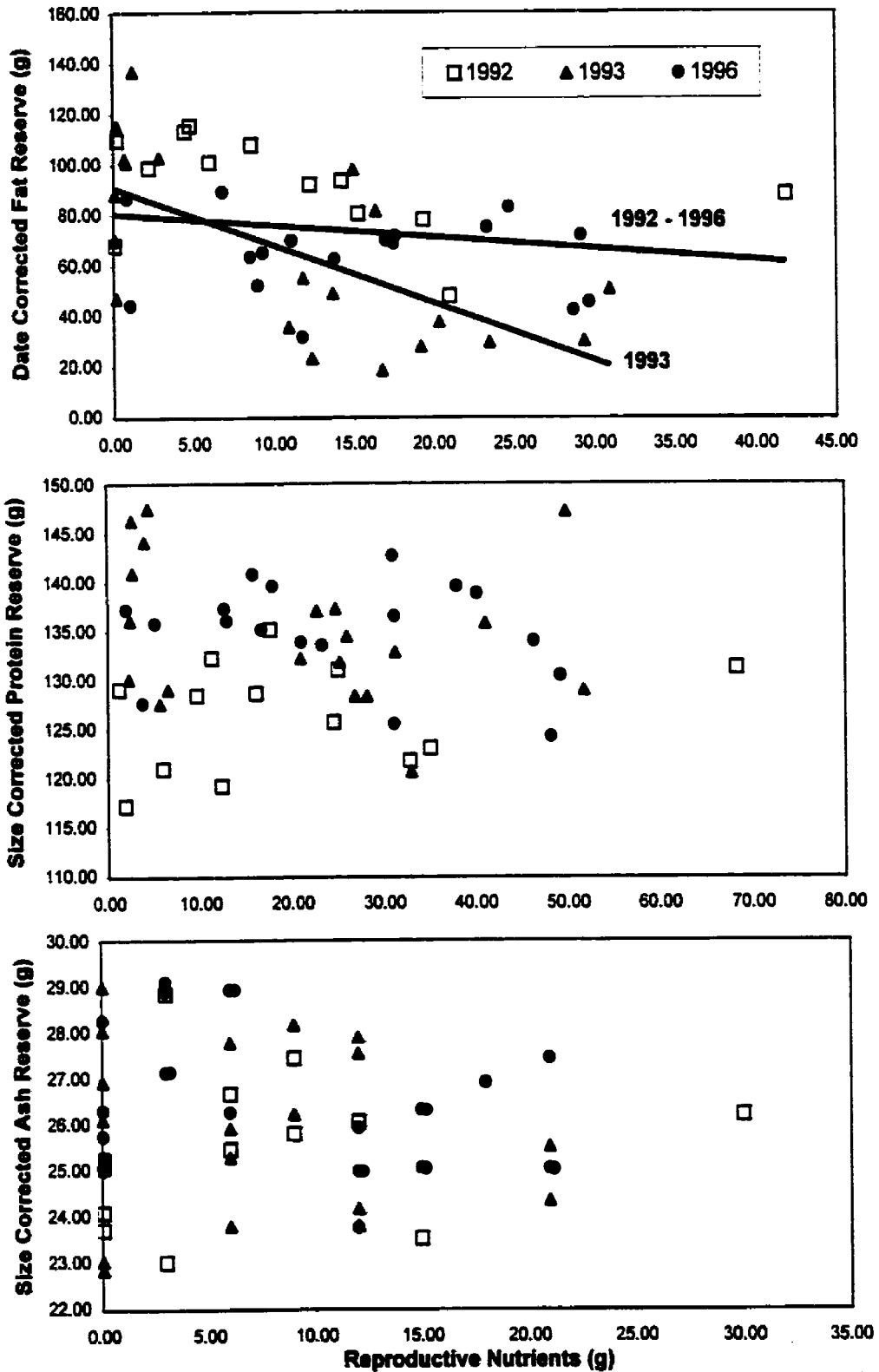

Figure 2.1. Nutrient reserves of RFG and Laying Northern Pintails in relation to nutrient investment in egg formation. Reproductive nutrients represent fat in the top, protein in the middle, and ash in the bottom graph. Fat reserves were standardized to a mean collection date of 30 April. Relationships were non-significant for protein and ash reserves.

Table 2.5. Analysis of covariance models describing changes in nutrient reserves relative to the amount of nutrient committed to reproduction (R-Nutrient), date of collection, year, and final clutch size for female Northern Pintails. Only females which had laid ≥ 3 eggs are included in sample.

Dependent	Model			Independent		
Variable	F	P	R^2	variable	F	P
Fat	2.73	0.06	0.49	Year	2.70	0.10
Protein	1.09	0.41	0.28			
Ash	0.80	0.57	0.22			

= 0.01). In general, pintails had the least amount of fat left at the end of laying and also committed the least amount of fat to clutch formation. Closer inspection reveals that pintails consistently fall below the regression line and drive the overall relationship (Figure 2.2).

2.4 Discussion

Similar to studies in Alaska (Mann and Sedinger 1993, Esler and Grand 1994b), I found that pintails relied on fat reserves during clutch formation more than any other duck species studied to date. However, unlike the Alaskan studies, I found no evidence that fat or protein reserve levels determined final clutch size. An interspecific comparison with 6 other dabbling duck species revealed that pintails had the least amount of fat left at the end of laying and invested the least amount of fat into a full clutch.

2.4.1 Muscle and Organ Dynamics

Change in size of digestive organs often reflects a shift in dietary strategy. Gizzard mass can decrease due to either decreased diet fiber content or metabolism of gizzard protein (Drobney 1982, Kehoe et al. 1988, Mann and Sedinger 1993). Decreased gizzard mass of ducks has been attributed to lower diet fiber content due to increased invertebrate consumption (Krapu and Reinecke 1992) and this may be the reason that gizzard mass decreased steadily from pre-RFG through laying. Although pintails consume primarily plant foods for the majority of the year (Martin et al. 1951), esophageal contents of RFG and laying females collected in North Dakota averaged 56% and 77% animal matter, respectively (Krapu 1974). It is unlikely that gizzard protein was metabolized since carcass protein was not utilized during clutch formation.

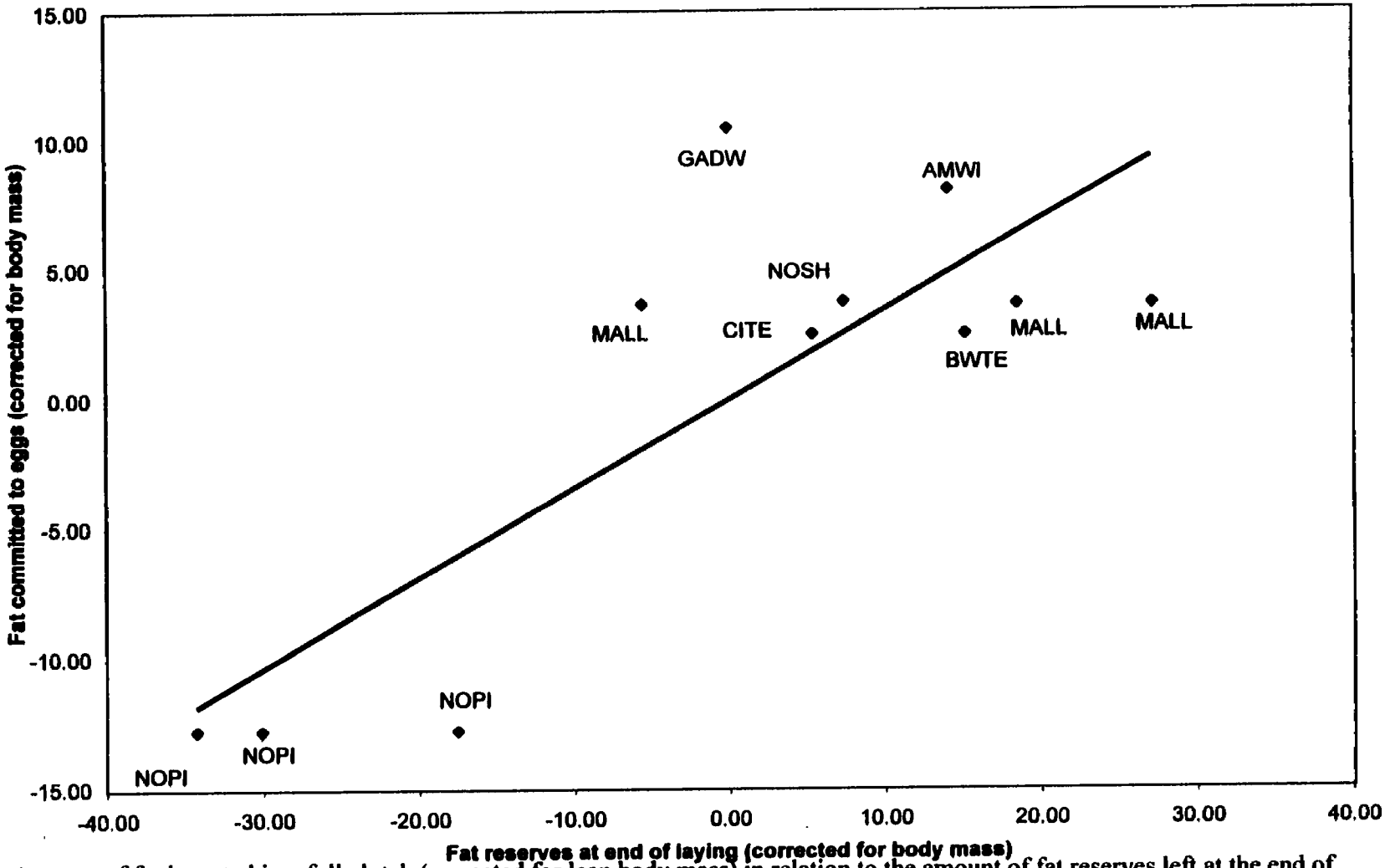

Figure 2.2. Amount of fat invested in a full clutch (corrected for lean body mass) in relation to the amount of fat reserves left at the end of laying (corrected for lean body mass) for seven dabbling duck species.

Increased food consumption and intermediary metabolism of fat and protein may increase liver mass in ducks (Drobney 1984, Ankney and Afton 1988, Heitmeyer 1988). Either of these factors may have influenced increases in liver mass of female pintails breeding in Alberta. Breast muscle mass was highest in RFG females, a finding also reported by Mann and Sedinger (1993). This may by due to greater flying associated with breeding behaviour; frequency of pursuit flights increases sharply just before egg laying begins (i.e., RFG) and continues until incubation commences (Smith 1968).

2.4.2 Nutrient Reserve Dynamics

Our work and that of Mann and Sedinger (1993) and Esler and Grand (1994b) found that pintails utilized fat reserves at a higher rate than any other duck species studied. Prior to my work, it was unclear whether reliance on fat reserves during clutch formation was an artifact of breeding in the Arctic or a phylogenetic trait. My data indicate that pintails breeding in prairie habitats also rely extensively on fat reserves during egg laying (at least for early-season clutches) and therefore this pattern of fat reserve use is species-specific. Pintails breed early in the season and reliance on fat reserves may be a physiological adaptation to accomplish this.

I found no evidence that either protein or ash reserves were utilized during egg laying. This is consistent with findings for most duck species, with the exception of Ruddy Duck (*Oxyura jamaicensis*), which uses both protein and ash (Tome 1984, Alisauskas and Ankney 1994), and species with primarily vegetarian diets (such as gadwall and American wigeon) which apparently cannot meet protein requirements exclusively via food consumption (Alisauskas and Ankney 1992).

The role of nutrient reserves in clutch size determination of ducks is controversial (Arnold and Rohwer 1991, Alisauskas and Ankney 1992). I found no indication that clutch size was limited by nutrient reserves. Fat and protein reserve sizes were unrelated to clutch size of females where I could estimate final clutch size. However, since sample ($n = 21$) and effect sizes were small, the reliability of this conclusion is low.

There is conflicting evidence regarding the role of nutrient reserves in determining final clutch size in pintails. A recent study on the Yukon Delta in Alaska reported that fat reserves proximately limited clutch size (Esler and Grand 1994b), but another Alaskan study at Minto Flats, claimed that clutch size was regulated by protein reserves (Mann and Sedinger 1993). Although these differences may be due to differences in analytical methods, it also suggests that generalizations regarding species-specific patterns of nutrient utilization should not be based on data from one year or study site.

I found evidence that species with the least amount of fat left at the end of laying also invested the least amount of fat in eggs (Figure 2.2). This relationship, however, is entirely driven by pintails, which have little fat left upon clutch completion, relative to the other dabbling duck species studied. This suggests that pintails must utilize a greater proportion of their fat reserves in order to lay a clutch. This strong reliance on lipid reserves during laying may allow females to maintain a high rate of egg production (one egg per day), while faced with shortfalls in dietary nutrients early in the season (Arnold and Rohwer 1991). The fact that pintails have little fat left at the end of laying may also help to explain why pintails have relatively small clutch sizes and lay few replacement clutches (Guyn and Clark 2000).

Pintails nest in the prairies, boreal forest and tundra, environments in which they are challenged by wide fluctuations in timing and duration of resource availability during the nesting period. I suggest that pintails high reliance on lipid reserves during clutch formation may allow them to nest early, an adaptation that enables them to cope with relatively short nesting seasons and variable environments.

CHAPTER 3. VEGETATIVE AND THERMAL CHARACTERISTICS OF NORTHERN PINTAIL NEST-SITES IN ALBERTA: IMPLICATIONS FOR NEST SELECTION AND SURVIVAL

3.1 Introduction

Birds typically do not distribute their nests randomly among habitats, and it is generally assumed that non-random placement results from natural selection (Southwood 1977). Since reproductive success strongly influences fitness, natural selection should favor nest choices that minimize reproductive failure (Martin 1993). Ground-nesting grassland birds usually suffer high rates of predation (Martin 1988, 1993, Beauchamp et al. 1996); therefore, tactics or traits that help nesting birds avoid predation should be favored (With 1994), particularly those that are learned rapidly or inherited (Endler 1986).

Researchers typically study how nesting habitat differs from available habitat (Wiens 1989). Nest-site selection, in terms of floristic composition or physiognomic features, has been studied for a wide variety of species (e.g., Lokemoen et al. 1984, Speiser and Bosakowski 1987, Badyaev 1995). However, the *pattern* of habitat use does not necessarily identify optimal nest-site choice if, for instance, not all potential nest-sites are available to an individual (Van Horne 1983, Sonerud 1985, Pulliam 1988) or current preferences reflect past, rather than ongoing selective pressures (i.e.,

evolutionary lag; Futuyma 1986). Contrasting habitat features of successful and unsuccessful nests can be useful in understanding the *process* of natural selection (e.g. Kelly 1993, Stokes and Biersma 1998, Clark and Shutler 1999). Successful nests are often better concealed than depredated nests (Crabtree et al. 1989, Martin 1992, Clark and Shutler 1999), but the strength of this relationship might depend on the predator community (e.g., Clark and Nudds 1991) and greater concealment might impose survival costs to parents (Götmark et al. 1995, Wiebe and Martin 1998). Here, I evaluate nest-site selection in northern pintails (*Anas acuta*), and determine whether patterns, if they exist, are consistent with site-selective predation on nests (Clark and Shutler 1999).

Amelioration of nest microclimate may also be an important consideration in nest-site choices by birds (e.g., Walsberg 1985), but putative thermal advantages of nest-site selection are rarely measured directly (e.g., Peterson and Best 1985, Beckoff et al. 1987, Sakai and Noon 1991, Gloutney and Clark 1997). The thermal environment of a bird's microhabitat, such as a nest, can have important ramifications in terms of energy budgets (Warkentin and West 1990, Novoa et al. 1990, Swain 1991). By selecting microclimates that reduce costs, birds may reduce energy requirements or reallocate conserved time or energy to other activities (Walsberg 1985, 1986, Webb and Rogers 1988) or future offspring (Kilpi and Lindstrom 1997). During incubation, when foraging and incubation requirements conflict, metabolic constraints may be intensified (Hogan 1989, Gloutney et al. 1993). Nesting birds may deal with this constraint by choosing nest-sites that minimize costs of incubation, an advantage that has been proposed to explain non-random nest-site selection in several species (e.g. Van Riper

1984, Bekoff et al. 1987, Van Riper et al. 1993), as well as interspecific differences in nest placement in ducks (Shutler et al. 1998). Nonetheless, evidence for microclimate selection by nesting ducks is generally lacking and equivocal (Gloutney and Clark 1997), so further work is needed to more fully test this hypothesis.

I studied Northern Pintails nesting in mid-grass prairie of southern Alberta, and this is one of the first studies to quantify nest-site characteristics of pintails. My first objectives were to determine nest-site selection in pintails, while simultaneously evaluating differences in vegetative and physical characteristics between successful and unsuccessful nests, females of different ages and sizes and seasonal variation in nest-site use. Pintails nesting in this area face widely varying temperature regimes during the breeding season. They begin nesting in April when temperatures are relatively cool and the area is characterized by strong westerly winds. However, their nesting season extends into early July when mid-day ambient temperatures often exceed 30 °C (note however, ground level temperatures would be expected to be much greater than this; see Gloutney and Clark 1997). During the first year of the study, I also noted that many pintail nest-sites were associated with either silver sagebush (*Artemisia cana*) or located in a depression. These depressions were typically small areas (< 0.5 m in diameter) that were lower (>10 cm) than the immediate surroundings (i.e., within a 1 m radius). Upland nesting ducks often construct a nest bowl prior to egg laying, but this is usually "a simple, shallow, hollowed-out depression" (Sowls 1955), typically only 2 – 5 cm deep (K. Guyn, pers. obs.). I hypothesized, therefore, that "depressions" and sagebushes might provide more favorable microclimates for nesting ducks. Therefore, my second set of objectives was to: 1) characterize the microclimate at pintail nest-sites;

2) determine if nest-site selection was based on microclimate (i.e., compare nest-sites to random sites); and, 3) assess if microclimates differed between depression versus sagebush nest-sites.

3.2 Methods

3.2.1 Study Area

Work was conducted on the Kitsim Ducks Unlimited Project (hereafter Kitsim) located near Brooks, Alberta (50°30'N, 112°3'W). Kitsim was constructed during 1980 - 1983, encompasses approximately 40 km^2, and contains a main reservoir and 65 managed wetland basins. Basins range in size from 0.5 to 24 ha with some containing small nesting islands measuring 40 x 18 m (Giroux 1981). Water in most basins was < 1 m deep, except for 1 - 2 m deep moats around islands. Basins are interconnected through a canal system that allows irrigation water to flow into them through the main reservoir. Depending on water availability, the basins are usually reflooded in mid-spring and late fall and some become dry by mid-summer. Upland habitat consisted of mixed-grass prairie, of the needlegrass (*Stipa*)-grama (*Bouteloua*) association (Coupland 1961), that was subject to seasonal grazing by cattle. Dispersed clumps of prickly pear (*Opuntia polyacantha*), ball cactus (*Mamillaria vivipara*) and silver sagebush were obvious vegetation components, together with ground lichens, moss phlox (*Phlox hoodii*), and pasture sage (*Artemisia frigida*). Crested wheat grass (*Agropyron cristatum*) dominates wetland dykes and revegetated pipeline rights-of-way. Emergent wetland vegetation is primarily cattail (*Typha latifolia*) and spikerush (*Eleocharis palustris*). Extensive oil development, consisting of existing well sites and active drilling, occurs throughout the eastern half of the Kitsim project.

Average annual precipitation is 341 mm (n = 28 years), with 50% of that occurring from April to July (long-term weather data were obtained from an Environment Canada station located near Brooks, Alberta); pintails initiate nests from mid-April to mid-June (Chapter 4). Monthly temperatures during the breeding season range from a mean minimum of -10.7 °C in April to a mean maximum of 33.4 °C in July (n = 28 years). Prevailing winds are from the northwest or southwest, with mean wind speed peaking in May at 17 km/h (n = 10 years). On average, April has the most days (14) with at least one hourly wind speed exceeding 30 km/h (n = 8 years). Temperature profiles during the pintail nesting season indicated that minimum temperatures did not consistently remain above 0°C until mid-May, 1996 and early-May, 1997. Temperatures first approached 30°C in early-June, 1996 and mid-May, 1997. Ambient temperature data during 1996 and 1997 was recorded on the study site using a Campbell Scientific 21X datalogger equipped with a CSI 207 temperature/relative humidity probe. Dataloggers recorded 60 min means based on 60 sec measurement intervals.

3.2.2 Nest Searching

During 1995-1996 all upland habitat on approximately 21 km^2 was systematically searched beginning in early May and ending in early July. Complete searches were conducted twice each season with an inter-search interval of approximately 28 days. In 1997, the search area was reduced to approximately 6.6 km^2, which allowed me to search the area 3 times, with 21 days between searches. Searches were conducted between 0730 and 1300 (Gloutney et al. 1993). A nest was defined as a bowl containing ≥ 1 egg and attended by a female when found (Klett et al. 1986). Upland

habitat was searched by 2-person teams using chain drags (9-mm-diam, by 80-m long) towed by two four-wheel drive all terrain vehicles, using procedures similar to those described by Higgins et al. (1969) and Klett et al. (1986).

Nests were revisited every 6-10 days until ≥ 1 egg hatched or the nest was abandoned or destroyed. A nest was considered successful if at least one egg hatched, as determined by presence of shell membranes (Klett et al. 1986) or ducklings in the nest bowl and unsuccessful if no ducklings hatched and evidence of predation was present. Abandoned nests were non-depredated clutches no longer tended by a female (eggs cold and no additional eggs deposited daily). As part of different study components, nesting females were trapped late in incubation using mist nets (Bacon and Evrard 1990), drop-door traps (Weller 1957) or walk-in traps (Dietz et al. 1994). The fifth secondary and middle secondary coverts were used to classify female age as second year (SY) or after second year (ASY), following Duncan (1985).

3.2.3 Nest-site Characteristics

Nest-site characteristics were based on nests found during 1995 and 1996 when the entire study area was systematically searched. When final nest fate was determined, vegetation composition and nest position were characterized at all pintail nest-sites not located on islands. I visually estimated the percent cover of various vegetation types (to the nearest 5%) within the area circumscribed by a fixed radius of 1m centered on the nest. Percent coverage was estimated for short-grass (e.g., blue grama [*Bouteloua gracilis];* ≤ 10 cm height), mid-grass (e.g., crested wheat grass; species generally > 10 cm in height), shrub (sagebush), bare ground, forb, lichen, cactus, cattail (*Typha*

latifolia), spikerush (*Eleocharis spp.*), litter, and moss phlox. In addition to vegetative features at the nest, I also measured the distance to the nearest shrub, documented whether the nest was located in a depression, and quantified the dimensions of the depression if present. To reduce observer bias, the same two observers took most measurements in both years, and both measured about equal numbers of nests and random sites.

To determine if pintails exhibited selective nest placement, I quantified vegetative cover and physical features of random sites, following the above methodology. Eighty random sites were measured, 40 in each of 1995 and 1996. Geographic coordinates of study site boundaries were determined with a hand held Global Positioning System (GPS) and random locations, bounded by these coordinates, were generated. The GPS unit was used to locate random sites in the field; sites landing in non-nesting habitat (i.e., water, roads) were dropped. At the random site, an observer tossed an object over their shoulder, and recorded at the landing site the same variables as for nests. To test for selective predation, I compared features of successful nests versus those destroyed by predators.

3.2.4 Thermal Environment

I monitored "black-body" temperatures at nest-sites that were no longer occupied (i.e., depredated or hatched), but during the period when pintails were still nesting. Black-body temperature is an index of temperature, that integrates heat transfer due to conduction, convection, and radiation (Clark et al. 1990). As measured in this study, "black-body" temperature provides a measure of heat load and is an index to operative

temperature. Thermal environments are often described using operative temperatures, a thermal index that allows single-number representation of an organism's complex thermal environment. Similar to black-body temperatures, operative temperature integrates heat transfer due to conduction, convection and radiation (Bakken et al. 1985, Clark et al. 1990) and can be measured directly using physical models of the animal of interest. These models explore the thermal environment at the same spatial scale that the animal experiences (Bakken 1992). The "model" that I used was a plastic bottle filled with 750ml of water (roughly equal to the weight of a female pintail) and painted to resemble the coloration and patterns of a female pintail. Although the "model" had different spectral properties than that of pintail feathers, this integrative method provided a better representation of heat load than air temperature alone (Gates 1980).

"Models" were placed directly into the nest bowl and always arranged along a north/south axis. To test if pintails were selecting sites with favorable microclimatic conditions, a random site adjacent to the nest-site was monitored concurrently. The random site was set up 5 m from the nest-site on a randomly selected bearing, placed in a shallow scrape mimicking a nest bowl, and again arranged along a north/south axis. Temperatures were monitored with a Chromal-Alumel thermocouple placed within each "model", and attached to a Campbell Scientific (CSI) 21X datalogger for continuous monitoring. Dataloggers recorded 30-min means and standard deviations based on 5-s measurement intervals. Prior to use, each sensor was simultaneously tested under similar conditions. Data were recorded at each setup for 4 to 5 days.

To assess whether nest-sites located in "depressions" experienced more favorable microclimatic conditions than those located near sagebushes, I concurrently monitored "models" in pintail nest-sites located in "depressions" and those associated with sagebushes. Therefore, at any one time, I had a pair (a nest-site and associated random site) monitored at both a "depression" and sagebush nest-site. By monitoring sites concurrently I was able to assess among-site differences under identical ambient conditions, obviating the need to control for weather conditions during analyses.

Energetic costs of incubation tend to increase linearly as ambient temperature falls below the lower critical temperature (T_{lc}; temperature below which animals must generate extra heat to maintain body temperature; Ricklefs 1974). The lower critical temperature is dependent on body size and can be determined from the equation

$$(40 - 4.73\ [\text{body mass (g)}]^{0.274}) \qquad (3.1)$$

(assuming a body temperature of 40°C; Calder and King 1974: equation 20). I determined the amount of time temperatures fell below this value at all sites.

3.2.5 Statistical Analyses

Nest-site Vegetation

Since cattail, cactus and spike-rush were found at few nests (< 7%), I deleted these categories in an effort to reduce the number of variables; therefore, vegetation composition does not equal 100% in tables. For pintail nest-sites, I first looked for temporal variation (year and measurement date) using MANOVA. Within a year, random sites were all measured within 7 days, so I only assessed annual variability. Characteristics of nest and random sites were also initially contrasted using MANOVA.

Since all random sites were located on the Kitsim study area, pintail nests located off of the study area were not included in any analyses that involved comparisons with random sites. Therefore, analyses based on pintail nests alone include a larger sample of nests found off Kitsim. Variables that discriminated between nest and random sites, and successful and destroyed nests, were identified by stepwise discriminant analysis. Before variables were used in the analysis, normality was assessed with Wilks-Shapiro tests. All coverage data were arcsine transformed and distance to nearest shrub was log transformed to improve normality. Variables were assessed for multicollinearity by examining the proportion of variance for each regression coefficient (and its associated variable) attributable to condition indices > 30 (Hair et al. 1995). Covariance matrices were tested for homogeneity using Box's M criterion (SPSS 1993). If within-group covariance matrices showed significant ($P < 0.05$) heteroscedasticity, the discriminant function analysis was then based on the group-specific covariance matrices. Maximization of the Mahalanobis distance (D^2) between the two groups was used as the criterion for variable selection in the stepwise procedure. Minimum tolerance level permitted was 0.001, minimum F to enter was 3.84 and maximum F to remove was 2.71. When sample size permitted, cross validation was conducted on 5 holdout groups and the results averaged. Holdout groups were created by randomly selecting twenty-five percent of the sample. Discriminant loadings, which measure the correlation between each independent variable and the discriminant function, were examined to determine the relative importance of each explanatory variable in discriminating between groups. All analyses were conducted using SPSS (1993).

Nest-sites and Female Characteristics

To test for a relationship between female size, nest initiation date, female age and nest-site characteristics, I first used principal components analysis (PCA) to help define the underlying structure in the data matrix. Due to small sample size and the chance of overfitting my data, I did not include the variable lichen, because it was absent from more than 80% of the sites, and when it was present, comprised < 8% of the sampled area. Since data normality is less problematic with PCA (Hair et al. 1995) no transformations were performed. I examined the anti-image correlation matrix (SPSS) to insure that PCA was an appropriate analysis method. Only principal components having eigenvalues > 1 were considered significant and retained. To improve interpretation of the principal components I used VARIMAX rotation. Principal components analysis (PROC PRINCOMP) using standardized measures of female head-bill length and wing length was used to provide an index of body size (PC1). I used ANCOVA to examine the relationship between female size index, female age, nest initiation date and each retained principal component. Unless stated, interaction terms were non significant. I also plotted all relationships to explore potential non-linear relationships.

Microclimate

Data were summarized as means and standard deviations for each microclimate site (nest and random) and time block (30 min period). I created a variable that coded for periods of darkness (2230 to 0430) and light (0500 to 2200). I adopted this approach because there is no insolation at night. The first 1/2 hour of data collected at each nest-site was deleted to allow for equipment equilibration. To insure that data were matched

by date and time I constructed a difference variable for each pair wise comparison. For nest vs. random sites I used the difference in mean temperature for every 1/2 hour period between a nest and its associated random site. For depression versus sagebush sites, I used the difference in mean temperature for every 1/2 hour period between concurrently monitored pairs of sagebush and depression sites. I used PROC MIXED (SAS 1996) to analyze microclimate data and assumed equal correlation or compound symmetry between all data points obtained from the same pair and period (darkness vs. light). The dependent variable was the constructed difference variable and fixed effects in the model were year, habitat, date, initiation date, day vs. night and initiation date*period. The random statement in the model identified the repeated measures and error structure of the data. A restricted maximum likelihood estimator was used for model selection. To assess differences in variability between random and nest-sites, and between depression and sagebush sites, the same analysis was repeated using the paired differences in mean standard deviation for each 1/2 hour block as the response. To illustrate temporal variability, I classified early nests as those initiated prior to 10 May and late nests as those initiated after this date; I then determined least square means for each initiation category and period (i.e., day versus night). To examine the proportion of time that nest-sites and random sites fell below/above critical temperatures I again matched data by date and time. I then cross-classified each pair of observations according to whether the nest and/or random site exceeded the given threshold. Appropriate for paired data, McNemar's test was used to assess statistical significance of the difference in probabilities of exceeding the threshold for the nest and random sites. All analyses were conducted using SAS (1996).

3.3 Results

3.3.1 Temporal Variation

The amount of mid-grass ($F = 10.2$, df = 1, 131, $P = 0.002$) and distance to shrub ($F = 2.9$, df = 1, 131, $P = 0.01$) varied between years at pintail nest-sites. There tended to be more mid-grass in 1995 (23.2% ± 31.8) than 1996 (8.9 % ± 17.4), and mean distance to nearest shrub was greater in 1995 (51.6 m ± 78.7) than 1996 (15.0 m ± 35.3). Other variables did not differ ($P > 0.1$). Within years, pintail nest-site characteristics did not vary with measurement date ($P > 0.5$).

At random sites the amount of lichen ($F = 19.1$, df = 1, 78, $P = 0.001$) varied between years, with more lichen in 1996 (3.6% ± 4.3) than in 1995 (0.8% ± 2.0). Other variables did not differ between years ($P > 0.1$). I did not test for within year differences at random sites, because all sites were measured in a span of six days each year.

3.3.2 Nest-site Characteristics

Pintail nests ($n = 114$) were dominated by short-grasses which comprised, on average, nearly 40% of the vegetation (Table 3.1). Forbs and mid-grass were the next most abundant vegetative types. About 1/3 of all pintail nests were located in depressions. Depressions ≥ 10 cm deep ($n = 39$) had a mean depth of 13.3 (± 0.4) cm and averaged 27.2 (± 1.7) cm in diameter. Median distance from nests to nearest shrub was 4.4 m (range = 0.1 – 200 m). In general, most features of pintail nests were highly variable.

Table 3.1. Percent coverage of predominant vegetation at Northern Pintail nests and random sites at Kitsim, Alberta, 1995 and 1996. Distance to nearest shrub and the number of sites located in depressions are also presented. Baregrnd = bare ground, Shrtgras = short-grass, Mid-gras = mid grass, Dst. Shr. = distance to nearest shrub, and Depress = depression.

Group	Baregrnd	Forb	Lichen	Litter	Shrtgras	Mid-Gras	Moss	Shrub	Dst. Shr	Depress[a]	n
Nest-Site											
Mean	11.5	11.4	1.9	7.5	39.4	12.7	4.7	6.5	13.2	39 (34.2%)	114
Std. D.	12.4	16.2	5.7	8.0	27.8	23.5	8.5	14.6	26.8		
Ran. Site											
Mean	8.4	5.9	2.2	5.7	49.5	0.9	25.1	0.9	6.1	5 (6.3%)	80
Std. D.	11.8	8.7	3.6	10.1	21.3	7.2	21.0	3.8	10.0		

[a] the number of plots that contained a depression in the 1-m circle

3.3.3 Nest-site Selection

Differences between nests and random sites (see Table 3.1) were first investigated using MANOVA. Nest-sites had less moss ($F = 83.0$, df = 1, 191, $P = 0.0001$), were more likely to be located in a depression ($F = 20.1$, df = 1, 191, $P = 0.0001$), had more shrub cover ($F = 10.3$, df = 1, 191, $P = 0.002$), less short-grass ($F = 10.4$, df = 1, 191, $P = 0.001$), more litter ($F = 7.1$, df = 1, 191, $P = 0.008$), more forb ($F = 7.1$, df = 1, 191, $P = 0.008$) and had more mid-grass ($F = 24.6$, df = 1, 191, $P = 0.0001$) than random sites.

The covariance structures of group matrices were not equal (Box's M = 104, $P = 0.0001$) so discriminant function analysis was based on group-specific covariance matrices. Four variables discriminated most strongly between pintail nests and random sites (Table 3.2). By inspecting the structure matrix loadings the amount of moss at the site was most important in distinguishing nests from random sites, with less moss cover occurring near nests (Table 3.1). The second most important discriminating feature was the presence of a depression; nests were more likely to be placed in a depression than random sites (Table 3.1). Pintail nests were also characterized by having less short-grass and more shrub cover. Cross validation using five holdout samples resulted in 87.1% of nests and 81.1% of random sites being correctly classified on average. The predictive validity of the discriminant function was further assessed by comparing the overall hit ratio (78.1%) with the proportional chance criterion (51.4%). Hair et al. (1979) suggests that the classification accuracy reflected in the overall hit ratio should be at least 25% higher than the proportional chance criterion (i.e., in this case it should be greater than 64.3%). Additionally, Press's Q statistic was significant (Press's Q =

Table 3.2. Correlation coefficients between discriminating variables and canonical discriminant function for Northern Pintail nest-sites versus random sites and successful versus unsuccessful nests (those which are underlined were retained in the final model), at Kitsim, Alberta, 1995 and 1996.

Variable	Random vs. nest sites	Successful vs. Unsuccessful
Bare ground	-0.09	0.18
Forb	-0.27	0.18
Lichen	0.12	-0.16
Litter	-0.35	0.08
Short-grass	0.30	-0.25
Mid-grass	-0.28	0.24
Moss	0.72	-0.30
Shrub	-0.20	-0.68
Distance to Shrub	0.02	1.00
Depression present	-0.39	0.01

44.26, $P < 0.001$) indicating that the predictions were significantly better than chance alone. Overall, I have strong evidence for non-random nest-site placement in pintails.

3.3.4 Nest Fate

Group covariance matrices were equal (Box's M = 0.38, $P = 0.54$) so I used the pooled covariance matrix. Distance to nearest shrub was the variable contributing most strongly to discrimination of successful and unsuccessful pintail nests (Table 3.2). Failed nests (22.8 m ± 51.3 SD) tended to be closer to shrubs than successful nests (58.6 m ± 82.4 SD; Table 3.3). Press's Q statistic indicated that predictions were significantly better than chance alone (Press's Q = 6.37, $P = 0.01$) but the overall hit ratio of 61.7%, was not 25% higher than the proportional chance criterion of 60.2%. This suggests that the predictive validity of the discriminant function may be low. Cross validation tests with hold out groups could not be run due to small sample size. In summary, I have weak evidence of non-random predation of pintail nest-sites.

3.3.5 Female Age

The sample used for this analysis relies on nests where the female was captured. Since females were only captured in late incubation, differences reflect nest-site characteristics of yearling versus older females that survived to late incubation; therefore, age-related processes occurring earlier in the nesting cycle would be missed. The covariance structure of the matrices for each group were not equal (Box's M = 13.0, $P = 0.006$) so discriminant function analysis was based on the group-specific covariance matrices. Nests ($n = 28$) of yearlings tended to have more mid-grass (20.0 % ± 5.6) and short-grass (38.6% ± 5.9) than did those of adults ($n = 42$; 10.4% ± 3.4,

Table 3.3. Percent coverage of predominant vegetation at successful and unsuccessful pintail nest-sites at Kitsim, Alberta, 1995 and 1996. Distance to nearest shrub and the number of sites located in depressions are also presented. Baregrnd = bare ground, Shrtgras = short-grass, Mid-gras = mid grass, Dst. Shr. = distance to nearest shrub, and Depress = depression.

Group	Baregrnd	Forb	Lichen	Litter	Shrtgras	Mid-Gras	Moss	Shrub	Dst. Shr	Depress*	n
Unsuccessful											
Mean	13.1	11.7	2.2	7.5	40.0	13.2	4.6	6.5	22.8	27 (39%)	77
Std. D.	15.3	17.9	6.4	7.7	28.6	23.8	8.4	14.8	51.3		
Successful											
Mean	18.1	12.2	0.8	9.4	30.0	16.5	3.9	4.8	58.6	8 (26%)	29
Std. D.	22.9	20.5	2.0	13.4	30.6	26.7	7.6	13.9	82.4		

* the percentage of plots that contained a depression in the 1-m circle

34.2% ± 4.5; respectively). Press's Q statistic indicated that predictions were significantly better than chance alone (Press's Q = 6.91, $P = 0.01$) and the overall hit ratio of 66.2% was 25% higher than the proportional chance criterion of 52%. Therefore, I have evidence for age-specific nest-site selection.

3.3.6 Female Characteristics and Nest Initiation Date

Principal component analysis produced 4 significant factors explaining 72% of the overall variance (Table 3.4). Examination of variable loadings on each principal component suggests that PC1 best describes a gradient or trade-off between amounts of mid-grass and litter versus short-grass. PC2 is best characterized by positive covariation between bare ground and distance to shrub; PC3 by a positive association with the presence of a depression and negative relationship with amount of shrub cover; and PC4 has a positive association with the amount of forb present.

Female body size (F= 5.3, $P = 0.03$, df = 1, 57) and age ($F = 3.9$, $P = 0.05$, df = 1, 57) were related to PC1 (Figure 3.1). The relationship between body size and PC1 suggests that larger birds tended to choose nest-sites that were not in depressions, with greater amounts of mid-grass and litter, less short-grass and farther from shrubs. There was also some evidence to suggest that younger females choose nest-sites with greater amounts of mid-grass and litter, but less short-grass. Female body size was also related to PC2 ($F = 7.2$, $P = 0.01$, df = 1, 57). However, closer examination of the relationship with PC2 revealed that two outlying points seemed to be driving the relationship. When

Table 3.4. Principal components resulting from the analysis of habitat variables at nests (n = 57) of Northern Pintails at Kitsim, Alberta, 1995 and 1996.

	PC1	PC2	PC3	PC4
Bareground	-0.22	0.91	-0.05	-0.06
Forb	-0.03	0.02	0.06	0.93
Litter	0.67	-0.11	-0.02	0.19
Mid-grass	0.82	0.09	0.06	-0.28
Short-grass	-0.56	-0.57	0.24	-0.16
Shrub	-0.21	-0.15	-0.89	-0.09
Hole	-0.46	-0.19	0.63	-0.13
Distance to Shrub	0.52	0.64	0.11	0.14
Moss	-0.46	-0.09	0.12	-0.43
Percent of total variance	30.7	15.2	13.2	12.6

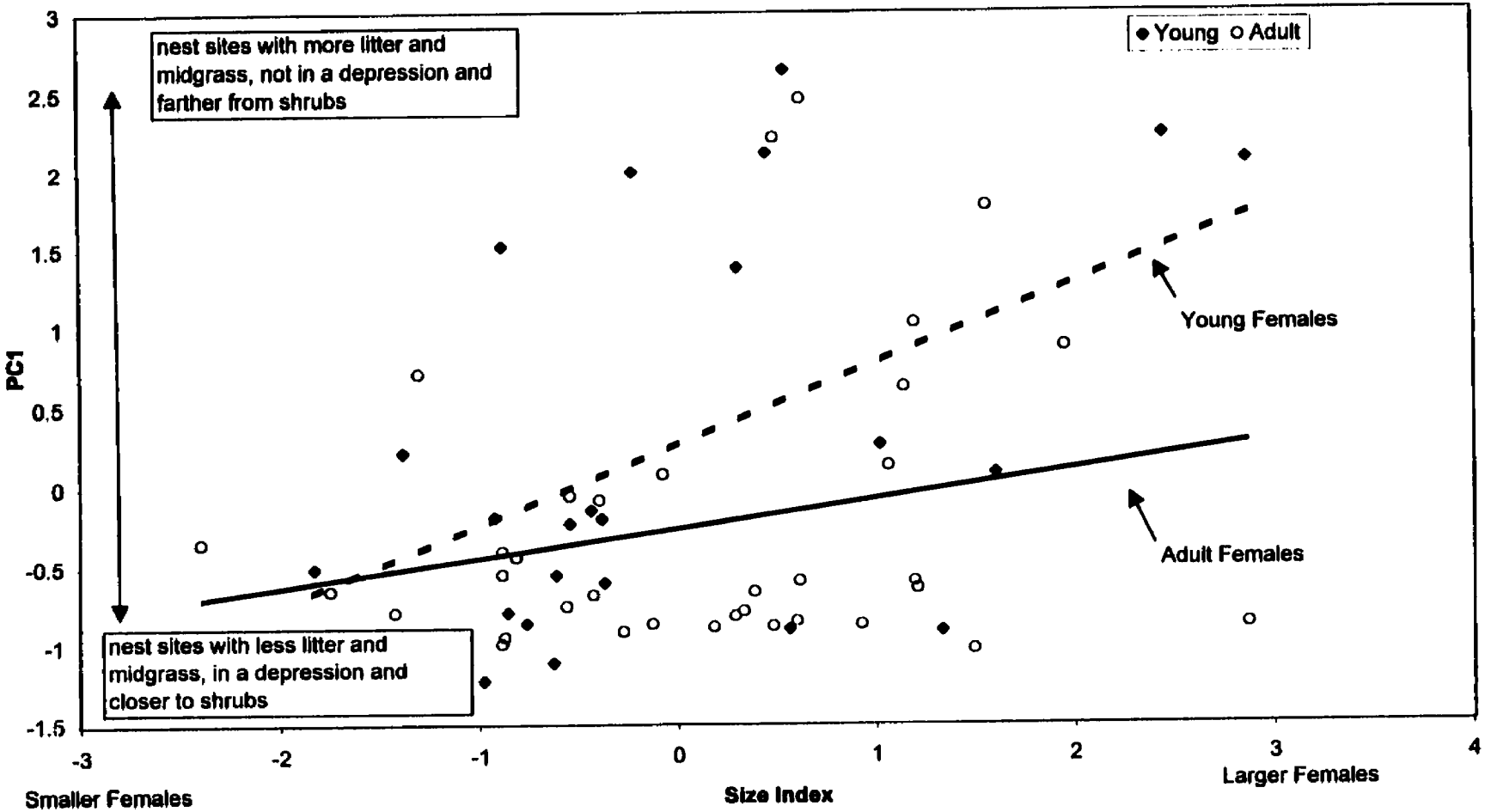

Figure 3.1. Regression of Principle Component 1 against female size index and age for Northern Pintails nesting at Kitsim, Alberta, 1995 and

these were removed a relationship did not exist ($F = 1.59$, $P = 0.21$, df = 1,55). Relationships with PC3 and PC4 were non-significant ($P > 0.2$).

3.3.7 Microclimate

Data were collected at 28 pintail nest-sites and 28 associated random sites (10 in 1996 and 18 in 1997). Of these, 13 were at nest-sites closely associated with sagebush and 15 were at pintail nest-sites located in depressions. Sites were monitored for a total of 26 days in 1996 and 54 days in 1997.

3.3.7.1 Nest versus associated random sites

Overall, mean temperature at nests (21.1 ± 0.18 °C) was about 1° C cooler than that of random sites (22.2 ± 0.21 °C) in 1997 ($F = 16.08$, df = 1, 12, $P = 0.002$), but not in 1996 ($F = 0.48$, df = 1, 12, $P = 0.50$). Irrespective of year, nests (25.4 ± 0.19 °C) were cooler than random sites (27.3 ± 0.20 °C) during daylight hours ($F = 20.52$, df = 1, 7361, $P = 0.0001$) but did not differ at night ($F = 2.34$, df = 1, 7361, $P = 0.13$). Mean difference in temperature between nest and random sites did not differ by habitat type ($F = 1.09$, df = 1, 12, $P = 0.32$). Mean difference in nest temperatures varied less at nests (0.64 ± 0.01 °C) than random sites (0.71 ± 0.01 °C) for pintail nests located near sagebush ($F = 30.58$, df = 1, 12, $P = 0.0007$), but not for nests located in depressions ($F = 1.25$, df = 1, 12, $P = 0.28$). Temperatures were less variable at nest-sites (0.75 ± 0.01 °C) than random sites (0.80 ± 0.01 °C) during daylight hours ($F = 20.61$, df = 1, 7361, $P = 0.0001$) but the two sites did not differ overnight ($F = 2.10$, df = 1, 7361, $P = 0.15$). Temperature variability did not differ annually ($F = 1.39$, df = 1, 12, $P = 0.26$).

I was also interested in temporal variation, specifically testing whether nests initiated early in the year were warmer than random sites and whether nests initiated later in the summer were cooler than random sites. I found a significant interaction between initiation date and period (day versus night; $F = 22.4$, df = 1, 7351, $P < 0.0001$). During daylight hours, nests initiated later in the summer tended to be cooler (3.0 ± 0.64°C) than their associated random sites, than nests initiated early in the summer (0.96 ± 0.46°C). However, at night, there was a weak trend for nests initiated early in the summer to be cooler than random sites (0.70 ± 0.47°C), while nests initiated later tended to be warmer than random sites (2.22 ± 0.65°C).

3.3.7.2 Depression versus Sagebush nest-sites

Mean temperature differences between concurrently monitored matched pairs of depression and sagebush nest-sites did not differ annually ($F = 0.41$, df = 1, 11, $P = 0.54$) or by period (day or night) ($F = 0.11$, df = 1, 3193, $P = 0.74$). Temperature variability also did not differ annually ($F = 0.01$, df = 1, 11, $P = 0.94$) or daily ($F = 2.40$, df = 1, 3219, $P = 0.12$). Given that year and period were not significant, I computed an estimate of the average difference between sage and depression nests (0.53 ± 0.44°C). Temperatures at matched depression and sage nests did not differ ($t = 1.19$, df = 3193, $P = 0.33$).

3.3.7.3 Critical Temperatures

Embryonic development ceases when egg temperature falls below physiological zero temperature (ca. 25°C; Haftorn 1988), whereas egg temperature above 41°C is lethal to embryos (Drent 1975). Thirty-minute mean temperatures exceeded the upper

lethal limit 16% of the time at random sites and 11 % of the time at nest-sites. I found that the probability of nest-sites exceeding 41 °C was less than the probability of random sites exceeding this level (McNemar's test: $\chi^2 = 241.1$, df = 1, $P < 0.001$). Nest-sites reached lethal temperatures most often (85% of the time) between 1300 and 1800. Nest temperatures often fell below physiological zero, reaching temperatures < 25 °C more often (64% of the time) than random sites (60%). The probability that a nest-site fell below 25 °C was greater than the probability of a random site falling below this level (McNemar's test: $\chi^2 = 184.1$, df = 1, $P < 0.001$). Nest-site temperatures typically (74% of the time) fell below physiological zero during 23:00 – 09:30.

If nest-sites are selected for microclimatic advantages (avoidance of temperatures < T_{lc} or those >40 °C) then one would predict that nest-sites would experience these conditions less often than random sites. Average female pintail body mass was 764 g (Guyn and Clark, unpubl. data), which translates to a T_{lc} of 10.8 °C. Nest-sites and random sites differed little in the amount of time they were below predicted T_{lc} (nest-site; 23.2%, random; 22.6%); however, the probability of nest-sites falling below this temperature was greater than that of random sites (McNemar's test: $\chi^2 = 6.1$, df = 1, $P = 0.01$).

3.4 Discussion

I tested three hypotheses (vegetation, female characteristics, microclimate) to explain patterns of nest-site selection in Northern Pintails, and obtained some evidence consistent with each of them. Ground nesting grassland birds often suffer high rates of nest loss due to predators, and pintails are no different (Beauchamp et al. 1996); during

my study, 37-45% of all pintail nests were destroyed by predators (Guyn and Clark 2000). Although selection of specific nest-site characteristics may help to reduce predation risk (Clark and Shutler 1999), the effectiveness of selective nest placement in deterring predators may depend on the types of predators in the system (Martin 1987b, Miller and Knight 1993). Overall, I found that pintails tended to choose nest-sites with greater shrub cover and mid-grass than random sites, and were more likely to be located in depressions. In general, this indicates that nest-sites were better concealed than random sites.

3.4.1 Vegetative Characteristics

I obtained weak evidence that nests most susceptible to predation were those associated with shrubs. A similar finding was reported for McCowan's Longspurs (*Calcarius mccownii*) nesting in the short-grass prairie of north central Colorado, where 75% of nests located near shrubs were depredated (With 1994). Although shrub cover provides good nest concealment, visual cover may be a more effective deterrent against avian than mammalian predators (Clark and Nudds 1991). In the short-grass and mixed-grass prairie, foraging rodents often use shrub cover (Murray and Vestal 1979, Kotler 1984, Kaufman and Kaufman 1989) and coyotes, which were common on the study area (K. Guyn, pers. obs.), may key into these areas for foraging. Regardless, experimental manipulation of shrub cover is required to reliably test these questions.

Were patterns of nest-site selection consistent with a predator-driven process, as indexed by differences between successful and depredated nests (e.g., Clark and Shutler 1999)? The answer to this question was equivocal. The most important variable

discriminating successful versus destroyed by predators, distance to shrub, was not important in distinguishing random sites from nests. Thus, further work is required to adequately resolve this question. However, differences in 8 of 10 variables used to segregate successful from destroyed nests were consistent with differences between nests and random sites (Binomial test, $P = 0.055$, one-tailed); successful nests were more similar to nests than to random sites, whereas destroyed nests were more similar to random sites than nests.

I found some evidence that female characteristics played a role in nest-site choice. Structurally larger females tended to choose nest-sites with taller grass cover, farther from shrubs and not located in depressions. Older females tended to chose sites with less mid-grass. Presumably larger birds chose nest-sites with taller grass cover to provide greater concealment. Since microclimate was only assessed at nests in depressions or associated with sage bushes, I was unable to determine if choosing taller grass reflects a choice based on microclimate or concealment. In general, however, pintails are renowned for nesting in sparse cover (Sowls 1955). Pintails frequent relatively flat or rolling grasslands (Austin and Miller 1995) and may trade-off concealment of eggs for a view of surroundings, possibly affording greater adult survival (Gotmark et al.1995, Wiebe and Martin 1998).

3.4.2 Microclimate

Nesting birds can respond to climatic extremes by selecting appropriate microclimates in which to nest and/or adapt nest structures to prevalent climatic factors (Horvath 1964). I found that nest-sites were cooler (about 2 °C on average) than

associated random sites during daylight hours. Furthermore, I found evidence that nests initiated later in the season were cooler than associated random sites, when compared with matched sites monitored earlier in the season. Because ground temperatures do increase during the season ($F = 11.2$, df = 1, 54, $P = 0.002$), females may adjust their nest-site choices based on seasonal temperature regimes to maintain more favorable microclimates.

Ground nesting birds may be subjected to extreme heat loading, either from direct solar radiation or from convective and conductive heat exchanges (Bartholomew and Dawson 1979, Dejong 1979, Goldstein 1984). Birds that nest in environments characterized by high daytime temperatures must invoke behavioral and physiological mechanisms to prevent themselves or their eggs from overheating (Ward 1990). Gloutney and Clark (1997) found that temperature and temperature variation did not differ between duck nest-sites and adjacent random sites. They suggested that within suitable nesting habitats chance events may exert such a strong influence that nest-sites and random sites might differ little with respect to vegetation and/or microclimatic conditions. Gloutney and Clark worked in Saskatchewan parkland habitat, a region that experiences hot, dry conditions less often than southern Alberta. The extreme climate of southern Alberta may exert a stronger selective pressure on nesting waterfowl, resulting in nest-site selection based, at least partly, on microclimatic characteristics.

The temperature range for optimum development of a bird's egg is narrow. In domestic fowl, for which development is best documented, the optimal temperature is 37 - 38°C (White and Kinney 1974, Drent 1975). Although egg development ceases below 25°C, embryos typically survive moderate cooling, but temperatures above 41°C

are almost always lethal (White and Kinney 1974, Drent 1975). It is therefore interesting to note that the probability of nest-sites reaching lethal temperatures was less than that of random sites. In some species, incubation is used to lower egg temperature during the heat of the day (Downs and Ward 1997). Further insight into this question may be gained by exploring incubation rhythms of pintails nesting in this environment.

In summary, I found that pintails exhibited non-random nest-site selection; however, differences between successful and unsuccessful nests were less readily discerned. In an open landscape, such as the grassland of southern Alberta, pintails probably rely on a suite of anti- predation tactics and behaviors. In an environment where lethal egg temperatures are common, females also exhibited nest-site selection based on microclimatic advantages, possibly affording advantages to the developing embryos.

CHAPTER 4. NESTING EFFORT OF NORTHERN PINTAILS IN SOUTHERN ALBERTA

4.1 Introduction

The amount of time and energy that individuals allocate to reproduction evolved in response to diverse selective pressures. Many species of northern temperate birds must breed, nest, and raise their young during a relatively short summer. In addition to season length constraints, environmental factors often vary temporally and can exert strong selective forces on reproductive effort and success. For example, initiation date and reproductive effort of waterfowl may be influenced by external forces such as seasonal temperature regimes and wetland conditions (Greenwood et al. 1995). Furthermore, early-nesting waterfowl produce larger clutches (Duncan 1987a, Blums et al. 1997a), may have greater nesting success (Flint and Grand 1996a), larger and faster growing young (Lindholm et al. 1994), greater fledging success (Guyn and Clark 1999), and higher local recruitment (Dzus and Clark 1998). Here, I evaluate variation in nesting effort and success of female Northern Pintails (*Anas acuta*; hereafter, pintail) breeding in a prairie habitat.

Nutritional requirements of egg laying are often hypothesized to constrain egg production (i.e., egg-production hypothesis), an argument that is frequently cited in clutch size theory of waterfowl (Ankney et al. 1991), but is strongly supported only for arctic nesting geese (Ankney and MacInnes 1978). Alternatively, factors related to timing of nesting may cause females to exercise restraint when forming eggs.

Production of additional eggs can have costs in terms of delayed hatching, because later hatching reduces chances of local recruitment (Dzus and Clark 1998). Furthermore, the laying of additional eggs may reduce opportunities for renesting due to either energetic or seasonal constraints. Thus, I examine whether there is a trade-off between larger first clutches and the amount of time required to lay a replacement clutch.

One of the most pervasive reproductive patterns in waterfowl and other birds is a decline in clutch size with initiation date (Rohwer 1992), a pattern often presumed to result from either renesting or delayed nesting by younger females, which in turn lay smaller clutches. However, smaller clutch sizes later in the season may be due to seasonally declining nutrient availability (Ankney and MacInnes 1978), or may reflect an attempt to reduce current reproductive investment in an effort to enhance future breeding potential (Hussell 1972). Therefore, I also test for a seasonal decline in pintail clutch size and look for relationships between current and future reproductive effort.

Egg size is an important determinant of reproductive investment. In most species of waterfowl, individual females show a high repeatability for egg size, suggesting that they cannot alter egg size in response to environmental conditions (Flint and Sedinger 1992). Egg size is thought to be an important reproductive trait because of its positive correlation with offspring survival (Thomas and Peach Brown 1988, Dawson and Clark 1996). Egg composition has been shown to vary allometrically with egg size, and therefore total clutch volume is a better predictor of nutrient investment in a clutch than is clutch size (Flint and Grand 1996b), so I assess variation in clutch volume while examining current versus future investment in eggs.

Nesting success is a critical determinant of productivity. Nesting success of pintails varies annually and geographically (Flint and Grand 1996a), resulting in wide differences in productivity among populations. For females that lose a clutch, renesting is an important strategy that enables females to increase the probability of reproductive success within years (Cowardin and Johnson 1979). Renesting propensity often is dependent on stage of incubation and date at the time of nest loss (Grand and Flint 1996a). I determine nesting success for pintails, test for annual differences, estimate renesting rate, and examine variation in renesting propensity.

Life-history traits of pintails differ from most other upland nesting ducks. Pintails are among the earliest nesting duck species (Bellrose 1980), and have one of the smallest clutch sizes (Austin and Miller 1995). Furthermore, the incubation period of pintails is relatively short (Bellrose 1980), and renesting persistence is reportedly low (Austin and Miller 1995). Detailed information on pintail reproductive characteristics is lacking, a deficiency identified in recent pintail population models (Carlson et al. 1993, Flint et al. 1998). During 1994-1997, I studied nesting and renesting ecology of pintails in southern Alberta. My objectives were to determine nest initiation dates, clutch sizes, egg volumes, nesting success, and renesting propensity. I compare my results to those from other studies of nesting pintail populations and discuss whether the pintail's unique reproductive traits are adaptations to the environments in which they breed.

4.2 Study Area and Methods

Field work was conducted on the Kitsim Ducks Unlimited Project land (hereafter Kitsim) located near Brooks, Alberta, Canada (50°30'N, 112°3'W) during 1994-1997. Kitsim was constructed during 1980-1983, encompasses approximately 40 km^2, and

contains a main reservoir and 65 managed wetland basins. Basins range in size from 0.5 to 24 ha with some containing small nesting islands measuring 40 x 18 m (Giroux 1981). Water in most basins was less than 1 m deep, except for 1-2-m deep moats around islands. Basins are interconnected through a canal system that allows irrigation water to flow into them through the main reservoir. Depending on water availability, basins are usually reflooded in mid-spring and late-fall, and some become dry by mid-summer.

Upland habitat consisted of mixed-grass prairie, of the needlegrass (*Stipa*)-grama (*Bouteloua*) association (Coupland 1961), which was subject to seasonal grazing by cattle. Dispersed clumps of prickly pear (*Opuntia polyacantha*), ball cactus (*Mamillaria vivipara*), and silver sagebush (*Artemisia cana*) were obvious vegetation components. Emergent wetland vegetation was primarily cattail (*Typha latifolia*) and spikerush (*Eleocharis palustris*). Extensive oil development, consisting of existing well sites and active drilling, occurs throughout the eastern half of the project land.

4.2.1 Nest Searching

During 1994-1996, all upland habitat on approximately 21 km^2 was systematically searched for nests beginning early May and ending early July. Complete searches were conducted twice each season with an inter-search interval of approximately 28 days. Searches were conducted between 07:30 and 13:00 (Gloutney et al. 1993). A nest was defined as a bowl with ≥ 1 egg tended by a female when found (Klett et al. 1986). Upland habitat was searched using procedures similar to those described by Higgins et al. (1969) and Klett et al. (1986). Nesting islands in all wetlands were searched on foot

at least once during late April or early May. Each time a nest was revisited on an island, the entire island was searched again. This ensured that most islands were searched every week until early July.

Nesting females were identified to species, and stage of incubation was determined by egg candling (Weller 1956). Nest initiation dates were calculated by subtracting the clutch size and number of days of incubation from the date of discovery (Sowls 1955). Nests were revisited every 6-10 days until ≥ 1 egg hatched or the nest was abandoned or destroyed. On each revisit the number of eggs and stage of development of embryos were recorded. On the last visit I assigned nest fate to one of five categories. A nest was considered successful if at least one egg hatched, as determined by presence of shell membranes (Klett et al. 1986) or ducklings in the nest bowl, and destroyed if no ducklings hatched and evidence of predation was present. Abandoned nests were non-depredated clutches no longer tended by a female (eggs cold and additional eggs not being deposited daily). For nests that appeared to be abandoned on the day of discovery, I attributed the abandonment to investigator activity. Nests were deemed nonviable if all eggs were infertile or embryos dead. Nest fate was unknown if the nest could not be relocated. Cause of nest failure was assigned to predation, weather, nest parasitism, fire, livestock, investigator activity, machinery, human activity, or unknown.

Clutch size for nests that survived to incubation was defined as the number of eggs laid in a nest. Clutch sizes of nests that had been parasitized (characterized by presence of Redhead [*Aythya americana*] or Mallard [*Anas platyrhynchos*] eggs in the nest bowl) or exhibited signs of partial nest predation were not used in analyses of clutch size.

Maximum lengths and breadths of all eggs in a full clutch were measured to the nearest 0.1 mm with dial calipers. Egg volume was calculated using the equation

$$\text{Volume} = -0.63392 + 0.53163(\text{length})(\text{breadth})^2 \text{ (Flint and Grand 1996b)} \quad (4.1)$$

4.2.2 Nest Trapping

I used mist nets or walk-in traps to capture nesting pintails late in incubation (Weller 1957, Bacon and Evrard 1990, Dietz et al. 1994). Body mass (nearest 10 g with a Pesola spring scale), wing chord length (nearest 1 mm with a ruler), and combined length of the head and bill (hereafter head-bill length; nearest 0.1 mm with dial calipers) were measured for all females. The fifth secondary covert was collected, and a visual inspection of the middle secondary coverts was used to classify females as second year (SY) or after second year (ASY), following Duncan (1985). I likely misclassified the age of some females (Esler and Grand 1994a). Given that misclassification was likely random, this error would reduce test power and not lead to false conclusions. Females also were fitted with a standard U.S. Fish and Wildlife Service leg band and nasal tags (Lokemoen and Sharp 1985).

4.2.3 Renesting

In 1997 I focused my study on renesting by pintails. I reduced the area searched for nests to approximately 6.6 km^2, enabling me to search the area three times with an interval of 21 days between searches. To obtain renesting estimates, I simulated a predation event by removing clutches from nesting pintails. Before clutches were removed, females were trapped using methods outlined above, and were banded, nasal marked, weighed, and measured. These females also were equipped with an 8-g

anchored backpack radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota) attached with a subcutaneous stainless-steel wire (anchor), glue, and three subcutaneous sutures (Mauser and Jarvis 1991, Pietz et al. 1995). The procedure was performed under local anesthetic (Lidocane), and was approved by the University of Saskatchewan Animal Care Committee (Protocol #940149) on behalf of the Canadian Council of Animal Care.

Females were caught and radio-tagged as early in the season as possible. I limited my sample to females with nests initiated prior to the average median initiation date of 16 May (Table 4.1). I assumed that these nests were most likely first nests. I attempted to capture females on or before 7 days of incubation, and was successful in capturing 90% of them before this day. Before females were released, all eggs were removed and the nest bowl destroyed.

To determine renesting effort, I used a truck-mounted null-peak antenna system (Kenward 1987) to locate radio-tagged pintails a minimum of twice daily, primarily during the morning (07:00-12:00) when laying females are likely to be found on their nests (Gloutney et al. 1993). If a female's position was triangulated to the same upland location for five consecutive mornings, the area was visited using a portable receiving system to determine whether the female was in nesting cover, rather than on a nearby wetland. If the female was in cover, she was flushed and the nest, if present, located.

After verifying that a radio-tagged bird was nesting, I monitored nest fate using telemetry. If the female was absent during the daily tracking session, another radio check was made later in the morning. If she again was not on her nest, the nest was visited to determine its status (hatched, destroyed, or abandoned).

Table 4.1 Number of nests, initiation dates, clutch size, and nesting success for Northern Pintails nesting near Brooks, Alberta, Canada, 1994 – 1996.

Parameter	1994	1995	1996
Number of nests	87	93	113
Median nest initiation	12 May	13 May	23 May
Range	7 April – 18 June	18 April – 17 June	13 April – 21 June
Median nest initiation upland	13 May	19 May	24 May
Clutch size	7.33 ± 0.16[a]	7.17 ± 0.16	7.05 ± 0.14
n	65	68	84
Upland nest success (%)	18.0	6.3	11.4
n	54	47	56
95% CI	9.8 – 32.7	2.3 – 16.1	5.6 – 22.6
Island nest success (%)	67.5	53.3	60.0
n	20	30	23
95% CI	45.8 – 99.0	35.3 – 80.2	38.2 – 93.6
Partial clutch loss[b]	16.6	50.0	11.7

[a]Mean ± SE; adjusted for initiation date.
[b]Proportion of successful nests which lost one or more eggs during incubation.

4.2.4 Decoy Trapping

To gather additional nesting information, pre-laying pintails were trapped during April 1994-1996 using decoy traps (Sharp and Lokemoen 1987). Traps were set in wetlands where pintail pairs were frequently seen, but to avoid capturing migrants I did not place traps on wetlands with large flocks (>50 birds). Once captured, females were marked, radio-tagged, and measured using techniques described above. Radio-tagged females captured in decoy traps were located twice daily between 07:00 and 13:00, from the morning following marking until late July. Locations and daily monitoring were conducted using methods previously described.

4.3 Statistical Analyses

Variation in initiation dates was examined using general linear modeling procedures (PROC GLM, SAS Institute 1996) to evaluate effects of year and female age. Multiple comparisons were performed using Tukey's studentized range test. Due to annual variation in nesting chronology, nest initiation dates were standardized for all further analyses by adjusting initiation dates each year to a mean initiation date of zero. Principal components analysis (PROC PRINCOMP) using standardized measures of female head-bill length and wing length was used to provide an index of body size (PC1). PC1 described positive covariation between the two original variables and accounted for 61% of the original variation. To assess whether the relationship between clutch size and initiation date was nonlinear, I used a lack-of-fit test to determine whether the second order term was necessary. Because clutch size typically declines with nest initiation date, I used analysis of covariance (ANCOVA; PROC GLM) with year and female age as main effects and female size index and adjusted initiation date

(and initiation date squared) as covariates. Total clutch volume was calculated as the sum of individual egg volumes within an incubated clutch. Variation in total clutch volume was examined using ANCOVA with year and female age as main effects and adjusted initiation date (and initiation date squared) and female size index as covariates. To examine the trade-off between egg size and clutch size, I examined variation in date-corrected clutch size (residuals from the clutch size versus initiation date regression) using ANCOVA with mean egg size as a covariate while controlling for possible year and female age/size effects. Current versus future investment in eggs was examined using full clutch information from individual adult females from two sequential years; date-corrected clutch size in year t+1 was regressed against date-corrected clutch size in year t. Similarly, initiation date in year t+1 was examined using ANCOVA, with covariates initiation date and clutch size in year t.

I estimated daily survival rates (DSRs) of nests by the Mayfield method as modified by Johnson (1979), first excluding nests that contained eggs that were broken by the investigator or abandoned due to my activity. Some nests were fenced to reduce predation for other components of the study (Guyn and Clark 1999), so these nests were also excluded from nesting success estimates. I estimated nesting success separately for island and upland nests, because island nests typically experience higher survival (Duebbert et al. 1983). To evaluate whether DSRs varied seasonally, I partitioned the number of exposure days, successes, and failures into early and late periods based on the annual median initiation date. I tested for variation in DSR across years, within years, and between island and upland nest locations following Sauer and Williams (1989). For ease of interpretation, I converted DSR to nesting success (P), where

$$P = (DSR)^I \quad (4.2)$$

and I = 32, the sum of average duration of laying period plus incubation interval in days (Klett et al. 1986).

I defined renesting interval as the number of days between the date of egg removal and the date the first egg was laid in a subsequent nest. For decoy trapped females, I used logistic regression (PROC LOGISTIC) to investigate the probability of renesting in relation to female age, past investment (number of days a nest was active), and date that the first nest was destroyed. Furthermore, I used multiple regression to examine the relationship between renesting interval, and the variables past investment and date of first nest destruction. For nest trapped females, I examined the relationship between female body mass at capture (corrected for size) and incubation stage with linear regression (PROC REG). Likewise, regression analysis was used to examine the relationship between initiation day of the first nest and female body mass. I used ANCOVA to investigate the relationship between renesting interval, and weight at capture, initiation day of first nest, female size index and age, and total clutch volume of the first clutch.

Values reported are means ± SE. Unless indicated otherwise, all 2-way interactions were tested and I used a significance level of $P < 0.05$.

4.4 Results

4.4.1 Nesting Ecology

Pintail nests ($n = 292$ during 1994-1996) were typically initiated over a 9-week period, with first nests appearing in mid-April (Table 4.1). Seasonal patterns of nest initiations were similar in 1994 and 1995, but were delayed in 1996 by approximately

10 days ($F_{2,292} = 6.4$, $P = 0.002$; Tukey's test, $P < 0.05$). When I included only nests where females were trapped, initiation dates did not differ by year ($F_{2,153} = 1.2$, $P = 0.3$) or female age ($F_{1,153} = 1.3$, $P = 0.3$).

Using all nests where full clutch size was determined, a quadratic term best described the relationship between clutch size and initiation date (lack-of-fit test, $F_{1,215} = 18.5$, $P < 0.001$; Fig. 4.1); clutch size did not vary with year ($F_{2,214} = 1.3$, $P = 0.3$) when initiation date was controlled. When I reduced the sample to include only those nests where I caught the female, full clutch size did not vary with female age, year or size of female (all $P > 0.1$) when initiation date was controlled.

I measured a total of 1,564 eggs with a mean egg volume of 39.85 ± 0.22 cm^3. Total clutch volume, adjusted for initiation date, did not vary with year, female age, or size index (all $P > 0.1$). I found no relationship between egg size and clutch size ($F_{1,106} = 0.04$, $P > 0.9$). Likewise, I found no evidence between years for a trade-off between current and future investment in eggs when I regressed date-corrected clutch size in year t+1 against date-corrected clutch size in year t ($F_{1,15} = 0.2$, $P > 0.6$). There also was no relationship between initiation date and clutch size in one year and initiation date in the next year ($F_{2,15} = 0.1$, $P > 0.8$).

4.4.2 Nesting Success

I detected no yearly difference ($\chi^2_2 = 1.9$, $P > 0.3$) in DSRs. Combined estimates (upland and island nests) of nesting success by year were 29.5% (1994), 22.0% (1995), and 19.5% (1996). Success was higher for nests located on islands than those located in upland habitats ($\chi^2_1 = 45.2$, $P < 0.001$; Table 4.1). Nesting success did not differ

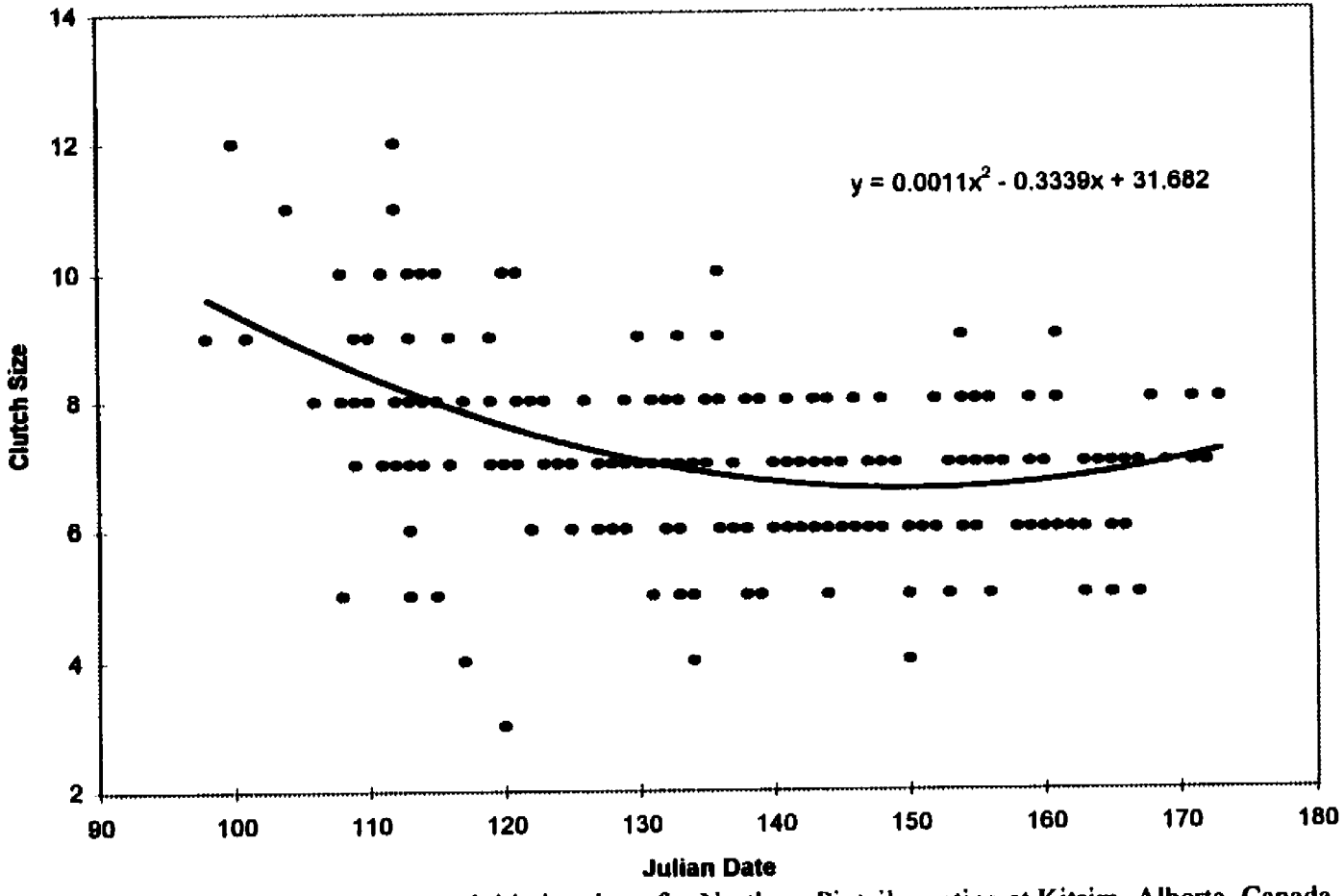

Figure 4.1. Regression of clutch size across nest initiation dates for Northern Pintails nesting at Kitsim, Alberta, Canada. Julian date 90 = 31 March.

among years for upland nests ($\chi^2_2 = 4.2$, $P > 0.1$) or island nests ($\chi^2_2 = 0.5$, $P > 0.8$). Based on annual median initiation dates, nesting success of upland nests did not vary between early and late nests ($\chi^2_1 = 0.8$, $P > 0.3$). The proportion of successful nests that lost one or more eggs during incubation varied from 12-50% during 1994-1996 (Table 4.1). The number of eggs lost did not vary with year or initiation date ($P > 0.3$). I estimate that predators destroyed 37-45% of all pintail nests (Table 4.2).

4.4.3 Renesting

4.4.3.1 Decoy Trapped Females

I captured 73 females in decoy traps during 1994–1996. Of these females, 55 were consistently tracked during the breeding season and 42 (76.3%) nested at least once. Fifteen nests subsequently hatched, leaving 27 females that could potentially renest. Of these, 20 were consistently tracked and 11 (55%) renested. Only one female renested twice. Analysis of renesting propensity was hampered due to quasicomplete separation of sample points, which prevented the determination of a maximum likelihood estimator in logistic regression. Further descriptive investigation revealed that probability of renesting was greater for those females that lost their nests early in the year. This analysis was based on a relatively small sample ($n = 20$), so results should be interpreted with caution. Renesting rate during the three years ranged from 36–67%, but these estimates did not differ ($\chi^2_2 = 2.2$, $P > 0.3$). For females that renested, nest initiation dates of first nests varied from 20 April to 21 May. Nest stage at time of destruction varied from laying to 11 days of incubation. The interval between first and second nest attempts varied from 2 to 29 days ($\bar{x} = 8.6 \pm 2.7$). Few clutches in this

Table 4.2. Fates (%) of Northern Pintail nests near Brooks, Alberta, Canada, 1994-1996.

Year	Successful	Destroyed	Abandoned	Investigator Abandonment[a]	Other[b]
1994	42.5 (34)[c]	37.5 (30)	12.5 (10)	3.8 (3)	3.8 (3)
1995	32.9 (28)	45.9 (39)	15.3 (13)	4.7 (4)	1.3 (1)
1996	41.1 (37)	41.1 (37)	13.2 (12)	3.3 (3)	1.1 (1)

[a] Hen flushed during laying (< 5 eggs), nest abandoned by next visit.
[b] Final nest fate unknown.
[c] Sample size.

sample were measured, therefore detailed analyses could not be performed; however, interval length was not related to past investment (number of days nest was active) or date the first nest was destroyed ($F_{2,9} = 0.8$, $P > 0.4$).

4.4.3.2 Nest Trapped Females

Twenty females were nest trapped and radio marked from 1 to 21 May 1997. Incubation stage at capture ranged from 3 to 8 days ($\bar{x} = 5.5 \pm 0.3$). Of these, three left the study area and four were killed (collisions with power lines) prior to renesting. Of the 13 birds remaining in the study sample, 11 (84.6%) initiated new nests, of which 3 were successful. Only two birds attempted a third nest; these two females were the only two that had abandoned their second nests. Although I could not conduct analysis of renesting propensity due to sample size limitations, the two females that did not renest "lost" their nest relatively late compared to others in the sample.

Female body mass at capture varied from 610-760 g, with a mean of 684.6 ± 9.2 g; body mass did not decline with increasing incubation stage ($F_{1,19} = 1.4$, $P = 0.2$), but incubation stage only ranged over 5 days. There was no relationship between female body mass during early incubation and initiation day of the first nest ($F_{1,19} = 0.1$, $P > 0.7$). The interval between first and second nest attempts varied from 7 to 38 days ($\bar{x} = 18.7 \pm 2.7$ days). Interval length rose markedly with increasing total clutch volume of the first nest ($F_{1,9} = 20.7$, $P < 0.01$; Fig. 4.2), but was not related to female body mass, size index, age, or initiation day (all $P > 0.1$).

4.5 Discussion

4.5.1 Nesting Ecology

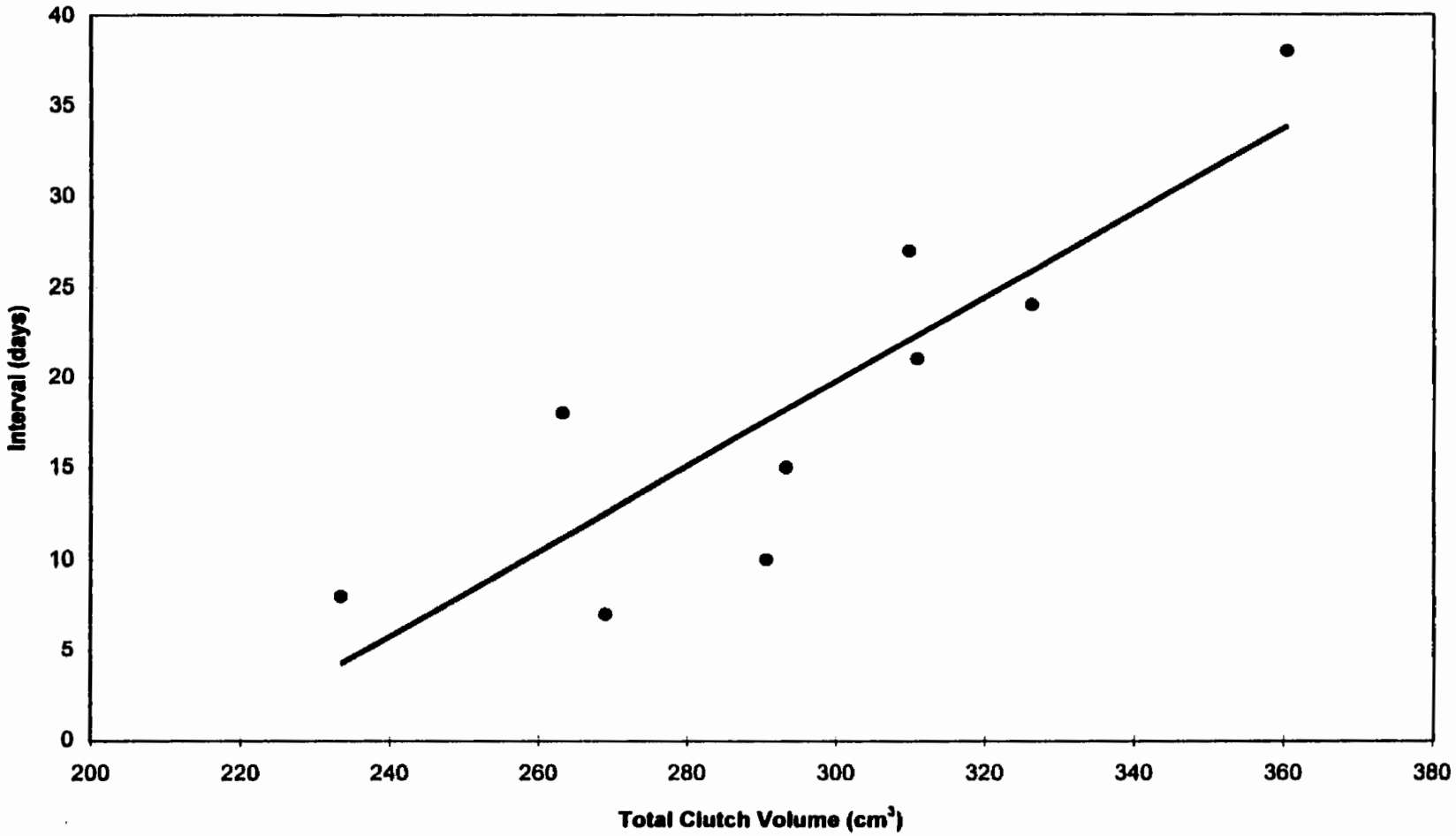

Figure 4.2. Renest interval length relative to total clutch volume of the first nest from Northern Pintails at Kitsim, Alberta, Canada.

Clutch size did not vary among years and was similar to that reported for pintails nesting on the prairies (6.9) (Duncan 1987a), but less than for pintails nesting in Alaska (7.63) and Manitoba (8) (Sowls 1955, Flint and Grand 1996a). Duncan (1987a) suggested that pintails in Alberta laid fewer eggs than pintails in Manitoba due to environmental constraint; but data to support his hypothesis were lacking. Nonetheless, the small average clutch size of pintails in this study (7.2), once again demonstrates that pintails lay small clutches compared to other prairie-nesting dabbling ducks.

The mean egg volume in this study (39.8 cm^3) was slightly larger than that found for pintails in Alaska (38.9 cm^3) (Flint and Grand 1996b) and for pintails nesting in Alberta (Duncan 1987b; predicted mean egg volume using equation from Flint and Grand 1996b = 38.6 cm^3). However, similar to Duncan (1987b) and Flint and Grand (1996b), I found no relationship between mean egg volume and clutch size. At the population level, it is interesting that pintails in Alberta tended to have larger eggs than pintails in Alaska, but produced smaller clutches. This suggests that there may be an intraspecific clutch-size vs. egg-size trade-off at the population level.

The rate of seasonal decline in clutch size was similar to that reported for other prairie nesting pintails but much less than for arctic breeders (Duncan 1987a, Flint and Grand 1996a). Flint and Grand (1996a) speculated that the seasonal decline rate in Alaska was steep due to a short breeding period. The breeding season in Alaska is roughly 20 days shorter (46 vs. 67 days) than in Alberta, a finding that is consistent with this idea. All work on pintails in Alberta (including this study) has been done on areas with managed wetlands. It is unclear whether the rate of decline in clutch size would

differ in non-managed areas, where, in most years, wetlands would be dry by mid to late summer.

4.5.2 Nesting Success

Duncan (1987a) reported that pintail nesting success was high (64%) on unbroken, grazed prairie; however, I studied pintails on large tracts of unbroken prairie and did not find higher nesting success than that found on areas of intensively farmed prairie (7%) (Greenwood et al. 1995). Although I believe that my estimates are unbiased, they may not be representative of mixed-grass prairie as a whole. Managed wetlands and oil and gas infrastructures (roads, powerlines, and well heads) were present on my study area and close proximity to large reservoirs may have had some impact on nesting success.

I found no seasonal difference in nesting success. In Alaska, pintail nesting success decreased seasonally, which was attributed to greater availability of alternative prey (i.e., other waterfowl nests) early in the season (Flint and Grand 1996a). Conversely, prairie nesting pintails are one of the earliest nesting ducks; therefore, there are few other waterfowl nests to function as alternative prey.

4.5.3 Renesting

Renesting is a strategy that enables ducks to increase within-year reproductive success (Cowardin and Johnson 1979). For ducks, which typically have reduced reserves available for renesting (Krapu 1981, Rohwer 1992), food quality and abundance on the breeding grounds may regulate a female's renesting ability (Krapu 1981).

Our renesting estimate for pintails in 1997 is the highest ever recorded for pintails, but was based on a limited sample of radio-tagged females (n = 13) and may therefore not differ from previously published estimates. Duncan (1987a) reported that only 5 of 127 (4%) color-marked and 0 of 17 radio-tagged females renested. However, in that study the detection rate of color-marked females was unknown and nests of radio-tagged females were destroyed at various stages of incubation. Grand and Flint (1996) removed clutches from radio-marked females at 4 ± 1 days of incubation and reported that 56% (22 of 39) renested. Grand and Flint suggested their estimate was probably low because some nests were likely destroyed before being detected and they were unable to monitor females that left the study area or those with failed transmitters. My renesting rate estimate from decoy trapped females was lower than my estimate obtained from nest trapped individuals. Unlike nest trapped birds, decoy trapped females tended to disperse off the study site making tracking more difficult. Therefore, it is possible that I may have missed some short renesting attempts, resulting in a lower renesting rate estimate. Although pintails have previously been thought of as infrequent renesters, my data and Grand and Flint's (1996) suggests that they will often attempt a second nest. Even though my sample size is limited, it appears that pintails rarely attempt more than two nests, unlike mallards which have been reported to nest up to six times (Rotella et al. 1993).

Interval length between first and second nests was positively correlated with total clutch volume of the first nest in 1997. Flint and Grand (1996b) found that total clutch volumes overlapped for clutches of different size and therefore suggested that total clutch volume was a better predictor of nutrient investment. Because egg composition

varies with egg size, females with larger clutch volumes in their first nests committed more nutrients to egg formation. Although renesting pintail females do not use endogenous nutrient reserves for clutch production (Esler and Grand 1994b), females may need to reach some threshold level of stored reserves, perhaps to complete incubation, before initiating a second nest. If this is true, one would then predict that those females which commit the most to their first clutch would take the longest to renest. Furthermore, given that clutch size/volume decreased seasonally, females may be attempting to decrease the interval between nest attempts later in the year. Longer renest intervals may have important implications for reproductive success, given that 10 and 30 day delays could result in 7% and 21 % reductions in duckling survival, respectively (Guyn and Clark 1999).

Pintails nest in the prairies, boreal forest and tundra, environments in which they are challenged by wide fluctuations in timing and duration of resource availability during the nesting and brood rearing periods. I suggest that pintail traits of early nesting, small clutch size, and low renesting persistence are adaptations that enable them to cope with relatively short nesting seasons and variable environments.

CHAPTER 5. FACTORS AFFECTING SURVIVAL OF NORTHERN PINTAIL DUCKLINGS IN ALBERTA

5.1 Introduction

Considerable attention has focused on nesting success of ducks, but much less is known about processes affecting brood-rearing and recruitment (Rotella and Ratti 1992a). Implicit in many studies is the assumption that nesting success is an appropriate measure of reproductive success (Greenwood et al. 1987), but recent evidence reveals much variation in post-hatch survival of ducks (see Grand and Flint 1996b for review). Thus, further work is needed to evaluate sources of variation in duckling survival and to more adequately assess individual reproductive performance. Here, I address this deficiency by looking at brood-rearing success of individually-marked female Northern Pintails (*Anas acuta;* hereafter pintail), and relating duckling survival to maternal and environmental attributes.

Unpredictable habitat conditions or severe weather events (occurring when ducklings are young) may induce substantial annual variation in duckling survival (Makepeace and Patterson 1980, Mendenhall and Milne 1985, Rotella and Ratti 1992a). Survival often declines with hatching date (Dow and Fredga 1984, Rotella and Ratti 1992a, Dzus and Clark 1998), a pattern which may arise because of seasonal deterioration in food resources, loss of wetlands, or lower maternal investment in brood

care (Sedinger and Raveling 1986, Rotella and Ratti 1992a), creating directional selection for early nesting. On the other hand, earlier nesting may be counterbalanced by lower survival in the earliest-hatched broods, producing stabilizing selection on nesting date (Rohwer 1992), a hypothesis which is rarely examined. In some species, older parents are better able to raise offspring, but age-specific analyses are limited in ducks (Hepp and Kennamer 1993, Blums et al. 1997a). Although evidence is limited, poorer survival of young in larger than average broods has been found for several waterfowl species (Leblanc 1987, Rockwell et al.1987, Dzus and Clark 1997b). Finally, some studies report a negative correlation between distance traveled overland and duckling survival (Ball et al. 1975, Rotella and Ratti 1992b), whereas others do not (Talent et al. 1983, Dzus and Clark 1997a). Thus, with respect to purported factors affecting duckling survival, there has been limited investigation and, in some cases, conflicting results have been obtained.

Therefore, my overall objective was to re-evaluate hypothesized sources of variation in duckling survival. Specifically, I tested whether survival varied annually and related this to wetland conditions. I also looked for a seasonal decline in survival, assessed whether survival might be related to female age or initial brood size, and then checked for a negative association between distances moved and survival.

5.2 Methods

5.2.1 Study Area

Work was conducted on the Kitsim Ducks Unlimited Project land (hereafter Kitsim) located near Brooks, Alberta (50°30'N, 112°3'W). Kitsim was constructed during 1980-1983, encompasses approximately 40 km^2, and contains a main reservoir and 65 managed wetland basins. Basins range in size from 0.5 to 24 ha with some containing small nesting islands measuring 40 x 18 m (Giroux 1981). Water in most basins was less than 1 m deep, except for 1-2 m deep moats around islands. Basins are interconnected through a canal system that allows irrigation water to flow into them through the main reservoir. Depending on water availability, the basins are usually reflooded in mid-spring and late fall and some become dry by mid-summer. Upland habitat consisted of mixed-grass prairie, of the needlegrass (*Stipa*)-grama (*Bouteloua*) association (Coupland 1961), which was subject to seasonal grazing by cattle. Dispersed clumps of prickly pear (*Opuntia polyacantha*), ball cactus (*Mamillaria vivipara*) and silver sagebush (*Artemisia cana*) were obvious vegetation components. Emergent wetland vegetation is primarily cattail (*Typha latifolia*) and spikerush (*Eleocharis palustris*). Extensive oil development, consisting of existing well sites and active drilling, occurs throughout the eastern half of the Kitsim project.

5.2.2 Trapping and Radio-tracking

Pre-laying, female pintails were trapped during April using decoy traps (Sharp and Lokemoen 1987). Traps were set in wetlands where pintail pairs were frequently seen, but I did not place traps on wetlands with large flocks of birds to avoid capturing migrants. To meet sample size targets for brood-rearing females (20 broods per year), I also trapped females on nests. Nests were located using an 80-m chain dragged

between two ATVs (Klett et al. 1986). Nesting females were then trapped late in incubation using mist nets (Bacon and Evrard 1990), drop-door traps (Weller 1957), or walk-in traps (Dietz et al. 1994). Mass (nearest 10 g, measured with a Pesola spring scale), wing chord length (nearest 1 mm, measured with a ruler), and combined length of the head and bill (hereafter head-bill length; nearest 0.1 mm, measured with dial calipers) were obtained for all females. The fifth secondary covert was collected, and a visual inspection of the middle secondary coverts (1995 and 1996 only) was used to classify females as second year (SY) or after second year (ASY), following Duncan (1985). I likely misclassified the age of some females (Esler and Grand 1994a). Given that misclassification error is likely random, this error would reduce test power and not false conclusions. Females were given a standard leg band, nasal tags (Lokemoen and Sharp 1985), and equipped with an 8-g anchored backpack radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota.) attached with a subcutaneous stainless-steel wire (anchor), glue, and three subcutaneous sutures (Mauser and Jarvis 1991). The procedure was performed under local anesthetic, and was approved by the University of Saskatchewan Animal Care Committee on behalf of the Canadian Council of Animal Care. Before being placed back on the nest, nest-trapped females were anesthetized using methoxyflurane to reduce capture-induced abandonment (Rotella and Ratti 1990).

Radio-tagged females captured in decoy traps were located twice daily between 07:00 and 13:00, from the morning following marking until late July. Locations were determined by triangulating from two positions using a vehicle-mounted null-array antennae system (4- or 5-element Yagi antennas; Kenward 1987). If a females position was triangulated to the same upland location for five consecutive mornings, the area

was visited using a hand-held receiving antenna to determine if the female was in nesting cover (i.e., rather than on a nearby wetland). If the female was in cover, she was flushed and the nest, if present, located. When a female's nest was found, she was located daily via telemetry to verify her presence at the nest. After full clutch size was determined, the nest was not revisited while the female was present.

Nesting females (decoy trapped and nest trapped) were monitored daily using telemetry to determine whether the female had left the nest. If a female was absent from her nest for two consecutive telemetry locations (approximately 3 hrs), I visited the nest to determine nest fate. If the eggs hatched, I determined initial brood size by subtracting the number of eggs that did not hatch from the last recorded clutch size. Broods were tracked daily and brood counts were attempted every 7 days until ducklings were 30 days old. If the observer was uncertain that all ducklings had been seen, counts were omitted. I assumed all ducklings were dead if, on two consecutive visits (1-2 days apart), the female was seen either with no ducklings or in an adult flock.

Distances from nest to nearest wetland were measured from air photographs, unless distance estimates were recorded on the original nest map (typically for nests located < 50 m from wetlands). All measurements were recorded as straight line distances. Nests located on islands were assigned a distance of 10 m.

5.3 Statistical Analyses

I tested whether brood size at hatch varied annually or with hatch date using analysis of covariance (ANCOVA; PROC GLM, SAS Institute, 1996). I defined brood survival as the proportion of broods with at least one duckling surviving to 30 days post-hatch. Variance was determined from a binomial distribution (SPSS, 1993).

Duckling survival was the proportion of hatched ducklings that survived 30 days. Duckling survival was estimated using a modification of the Mayfield method (Flint et al. 1995a). One of the assumptions of the Mayfield method is that survival is constant through the period of observation. Ducklings often experience high mortality early in brood rearing and inspection of survival curves from this study suggested that most pintail duckling mortality occurred prior to 7 days post-hatch. Therefore, I estimated daily survival rates for ducklings < 8 days of age and ducklings 8 to 30 days old. The 30-day survival estimate was the product of the survival estimates for the two periods (Johnson 1979). To address the problem of non-independence of brood mates, variance of the duckling survival rate was based on results for cluster sampling with individual broods treated as clusters (Flint et al. 1995a). Variation associated with this survival estimate was calculated following Goodman (1960) and DeMaso et al. (1997). A chi-square test for independent survival rates was used to compare daily survival rates among years (program CONTRAST: Sauer and Williams 1989). Variation in daily survival rate with duckling age was determined using conditional probabilities of mortality and exposure (Klett and Johnson 1982), where conditional probability of an observed change was calculated using methods in Grand and Flint (1996b). The product of individual daily survival rates produced an estimate of the survival function and cumulative estimates of duckling survival (Klett and Johnson 1982, Flint et al. 1995b).

To correct for date effects on initial brood size at hatch, I used the residuals derived by regressing brood size at hatch against hatching date. Residuals rather than initial brood size were then used in all subsequent analyses. To examine inter-brood

variability in survival, a duckling survival estimate also was calculated on a per brood basis (above). Distance from nest to nearest wetland was log transformed to improve normality.

Logistic regression (PROC LOGISTIC; SAS Institute 1996) was used to evaluate brood survival (at least one duckling survived versus none) in relation to the following six attributes: (1) year, (2) female age (SY vs. ASY), (3) hatch date, (4) hatch date squared, (5) distance from nest to nearest wetland, and (6) brood size at hatch (residuals). Variables 1 and 2 were categorical, the remaining were continuous. I limited analyses, *a priori*, to two-way interactions, and further limited interactions to those involving main effects and covariates. I used the Akaike Information Criterion (AIC) (Akaike 1985, Burnham and Anderson 1992) with the small-sample bias adjustment

$$IC_c = AIC + [(2p(p + 1))/n - p - 1)]) \text{ (Hurvich and Tsai 1995)} \qquad (5.1)$$

to choose the models that best fit the data. I started with a set of 25 candidate models and selected the model or family of models with the lowest AIC score(s) as the best model(s). If two or more models had similar AIC values, I chose the model with the fewest parameters, based on the principal of parsimony.

Analysis of covariance was performed to evaluate sources of variation in duckling survival rate (per brood), using the same explanatory variables. For this analysis, I used the same model selection criteria used in the brood survival analysis based on a set of 44 candidate models. AIC scores were derived from sum of squares error (SSE) using the formula

$$(n)[\ln(SSE/n)]+2p \text{ (SAS Institute 1996)} \qquad (5.2)$$

where n is the sample size and p is the number of model parameters, including the intercept. AIC_c scores were then calculated. Unless stated otherwise, I report least squares means and standard errors derived from ANCOVA when comparing groups.

All results are reported as mean ± SE, and I used $P < 0.05$ as my level of accepted significance.

5.4 Results

I trapped and radio-tagged a total of 65 females. Because few decoy-trapped females nested successfully, the majority of my sample consisted of nest-trapped females. I excluded eight females where brood counts were not obtained , three females that lost transmitters, and two that experienced nest destruction prior to hatch. I obtained data from 57 brood-rearing females that successfully hatched 383 ducklings (Table 5.1). Yearlings (SY) comprised 31, 38, and 18% of the sample in 1994, 1995 and 1996, respectively, but this variation was not significant ($\chi^2_2 = 2.2$, $P > 0.3$). Initial brood sizes at hatch did not vary among years (ANCOVA, $F_{2,55} = 2.2$, $P > 0.1$), but did decrease with hatch date ($F_{1,56} = 13.00$, $P < 0.001$, Fig. 5.1). Hatch dates spanned 50, 38, and 36 days in 1994, 1995, and 1996, respectively, but did not differ among years (Kruskal-Wallis test, $\chi^2_2 = 0.5$, $P > 0.7$). Distance from nest to nearest wetland varied from < 10 m to 1500 m, but 72% of all nests were located ≤ 100 m from wetlands, with no differences among years (Kruskal-Wallis test, $\chi^2_2 = 1.1$, $P > 0.5$).

Brood survival did not vary among years ($\chi^2_2 = 1.4$, $P > 0.4$), at 0.88 ± 0.08, 0.72 ± 0.11, and 0.82 ± 0.08 for 1994, 1995 and 1996, respectively. The model with the lowest AIC_c score (Table 5.2; $AIC_c = 53.99$) indicated that brood survival declined with

Table 5.1. Method of capture and age ratio of brood hens, average (± SE) brood sizes at hatch and hatch dates of Northern Pintails at Kitsim, Alberta, 1994-1996.

	Method of Capture					Hatch Dates		
Year	decoy	nest	total	SY:ASY	Brood Size	first	last	median
1994	2	15	17	5:11[a]	7.0±0.5	11 May	30 June	9 June
1995	5	13	18	7:11	5.9±0.4	23 May	30 June	10 June
1996	3	19	22	4:18	7.1±0.4	20 May	25 June	6 June
Total	10	47	57	16:40	6.7±0.2	11 May	30 June	11 June

[a] One female could not be aged.

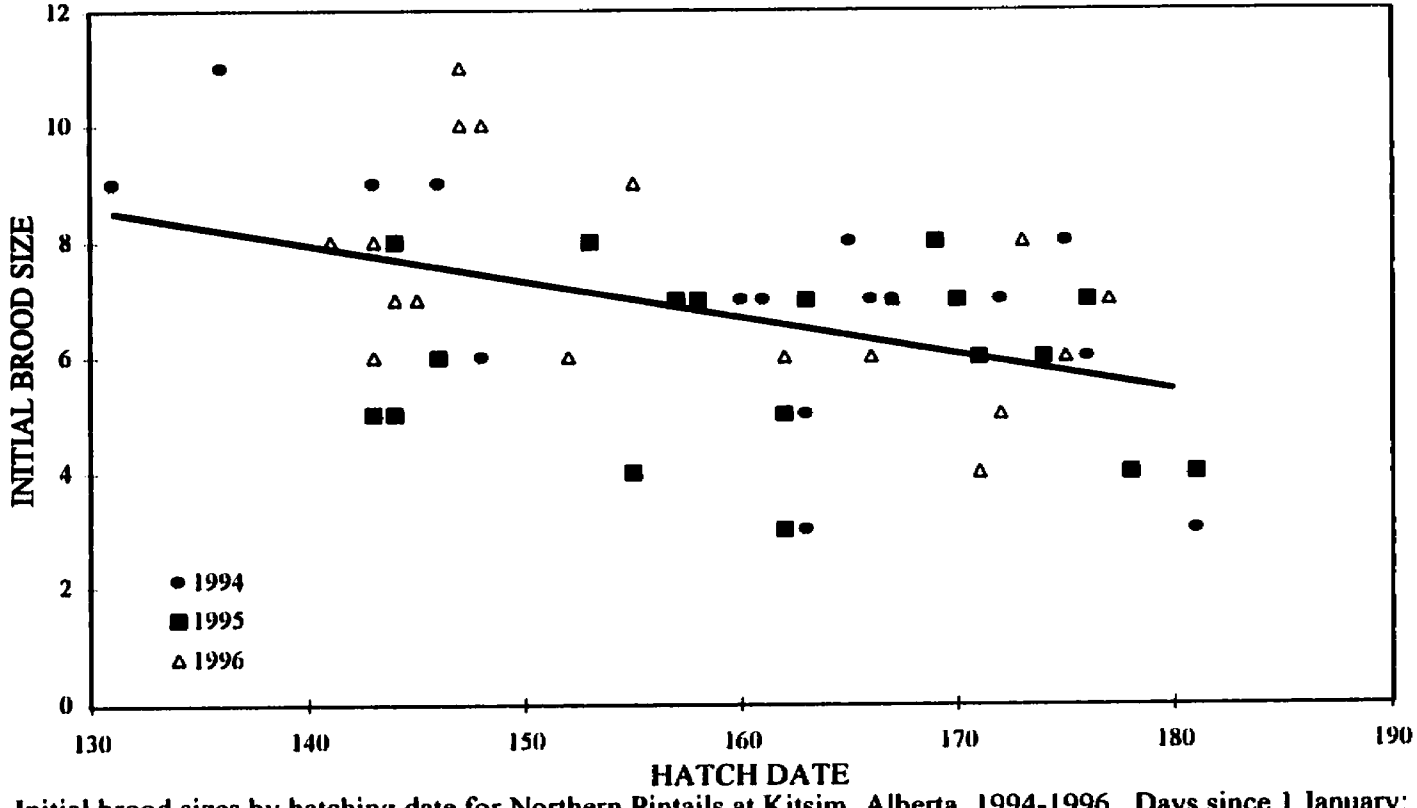

Figure 5.1. Initial brood sizes by hatching date for Northern Pintails at Kitsim, Alberta, 1994-1996. Days since 1 January: day 130 is 9 May and day 180 is 28 June.

Table 5.2. Akaike Information Criterion (AIC_c) values, adjusted for small sample size, for representative models of 30-day survival of Northern Pintail broods near Brooks, Alberta, 1994 - 1996. Analyses were based on logistic regressions.

Model	NP[a]	AIC_c[b]
Hatch Date	**2**	**54.0**
Distance to Wetland	2	58.6
Age	2	59.7
Initial Brood Size	2	59.1
Year	2	60.0
Hatch Date, Hatch Date Squared	3	54.8
Hatch Date, Distance to Wetland	3	54.8

[a] Number of parameters in model.
[b] Models with the lowest AIC value are optimal and indicated by bold-faced type.

hatch date; successful broods hatched about 10 days earlier than unsuccessful broods (mean hatch dates: June 5 ± 12 days vs. June 15 ± 12 days).

Although duckling survival to 30 days appeared to vary annually (1994; 0.65 [CI 0.29-1.00], 1995; 0.42 [CI 0.11-1.00], 1996; 0.44 [CI 0.12-1.00]), being substantially greater in 1994, there was no difference among years (Program Contrast; $\chi^2_2 = 0.5$, $P > 0.7$). Daily survival rate did not differ among years in either the ≤ 7-day-old age category ($\chi^2_2 = 5.0$, $P > 0.08$) or the 8-30-day-old age group ($\chi^2_2 = 0.5$, $P > 0.7$). However, daily survival rate was higher for older (8-30 days) ($\chi^2_1 = 20.2$, $P < 0.001$) than younger (< 8 day-old) ducklings. Duckling mortality was greatest during the first 7 days post hatch in all years (Fig. 5.2), estimated as 60, 76, and 76% of all losses during 1994, 1995 and 1996, respectively.

The model best describing duckling survival included hatch date, year, initial brood size and an interaction between initial brood size and year (Table 5.3, $AIC_c = -132.2$). Although the model which included distance to wetland had a similar AIC value (-132.3), I chose the simpler model (i.e., fewer parameters) based on the principal of parsimony. Ducklings which hatched earlier in the season had better survival than those hatched later (Fig. 5.3). Closer examination of the interaction between initial brood size and year revealed that duckling survival tended to be higher for larger initial broods in 1994 but lower in 1995 and 1996 (Fig. 5.4).

5.5 Discussion

5.5.1 Brood and Duckling Survival

My 1994 duckling survival estimate (65%) for pintails is one of the highest reported for waterfowl, but, in 1995 and 1996, survival fell more than 20% to values

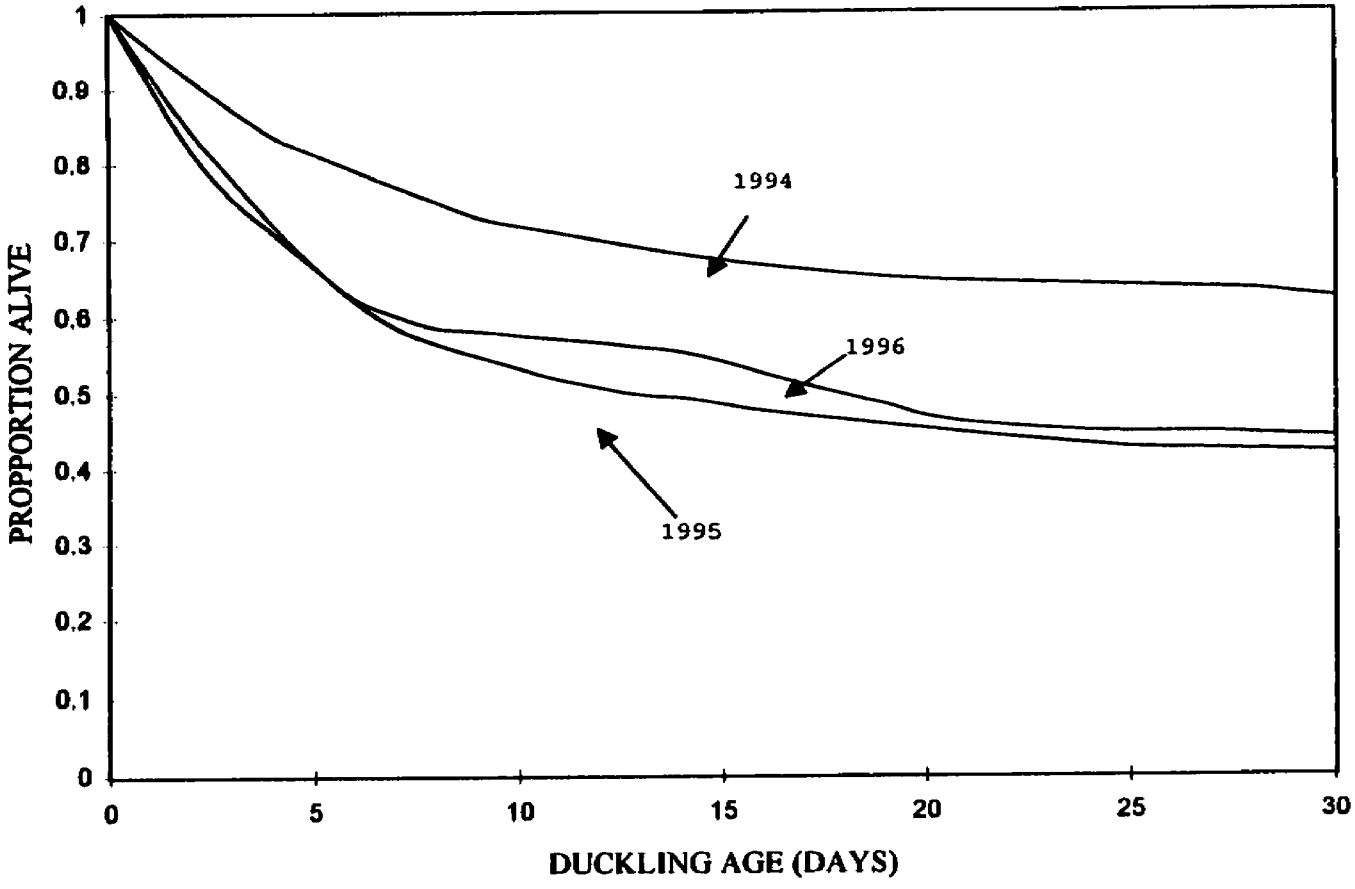

Figure 5.2. Proportion of Northern Pintail ducklings surviving by age at Kitsim, Alberta, 1994-1996.

Table 5.3. Akaike Information Criterion (AIC_c) values, adjusted for small sample size, for a confidence set of models of 30-day survival of Northern Pintail ducklings near Brooks, Alberta, 1994 - 1996.

Model	NP[a]	AIC[b]
Year, Init. Brood Size, Hatch Date	5	-130.5
Year, Init. Brood Size, Dist. Wetland, Hatch Date	6	-130.1
Year, Init. Brood Size, Hatch Date, Hatch Date Squared	6	-128.8
Year, Init Brood Size, Hatch Date, Hatch Date Squared, Dist. Wetland	7	-129.3
Year, Init. Brood Size, Hatch Date, Init. Brood*Year	7	**-132.2**
Year, Init. Brood, Hatch Date, Hatch Date Squared, Init. Brood*Year	8	-131.0
Year, Init. Brood Size, Hatch Date, Dist. Wetl., Init. Brood*Year	8	-132.3

[a] Number of parameters in model.
[b] Akaike information criteria were used to evaluate models; the model with the lowest AIC value is optimal and indicated by bold-faced type.

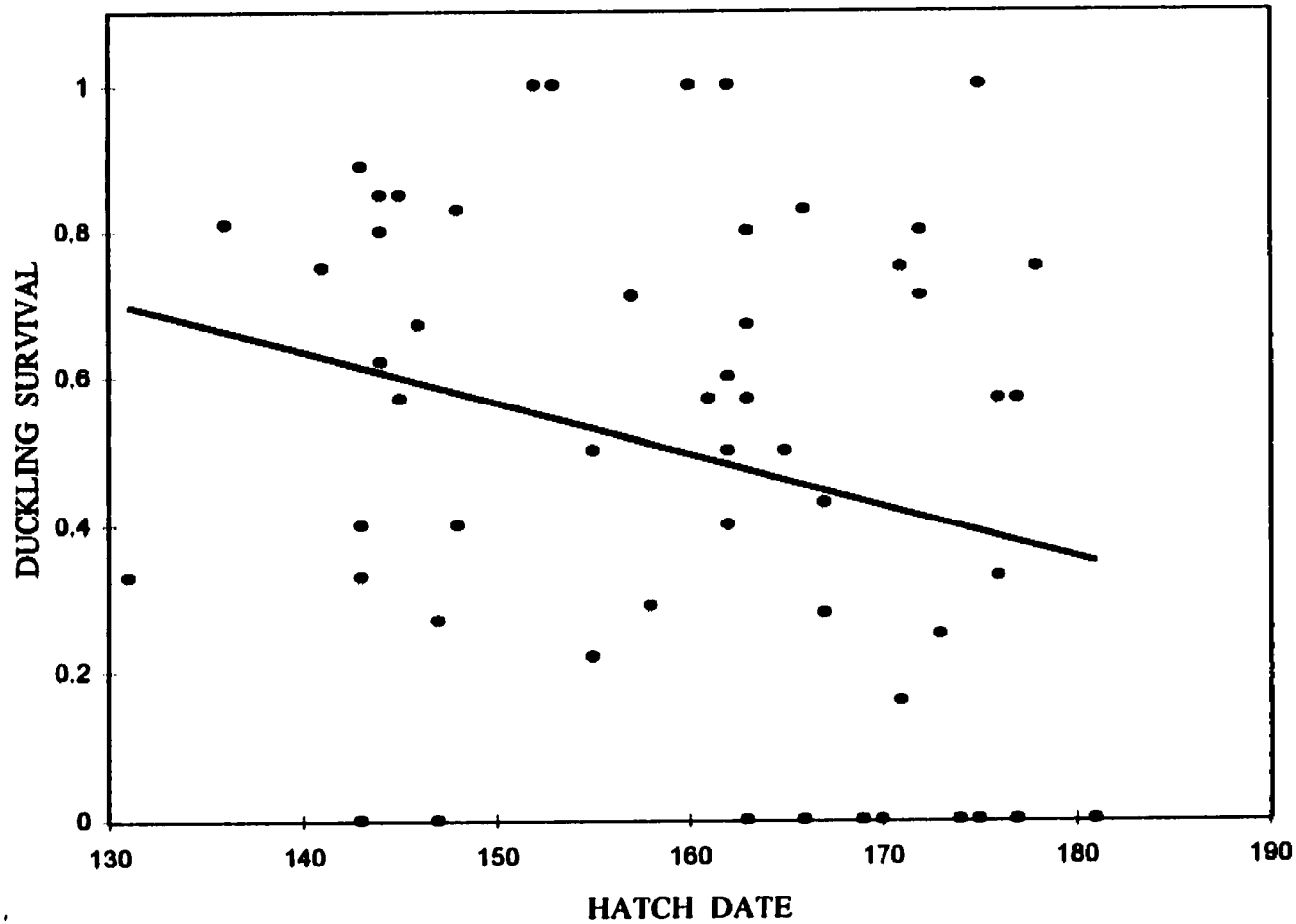

Figure 5.3. Northern Pintail duckling survival, 1994-1996, by hatching date at Kitsim, Alberta. Days since 1 January: day 130 is 9 May and day 180 is 28 June.

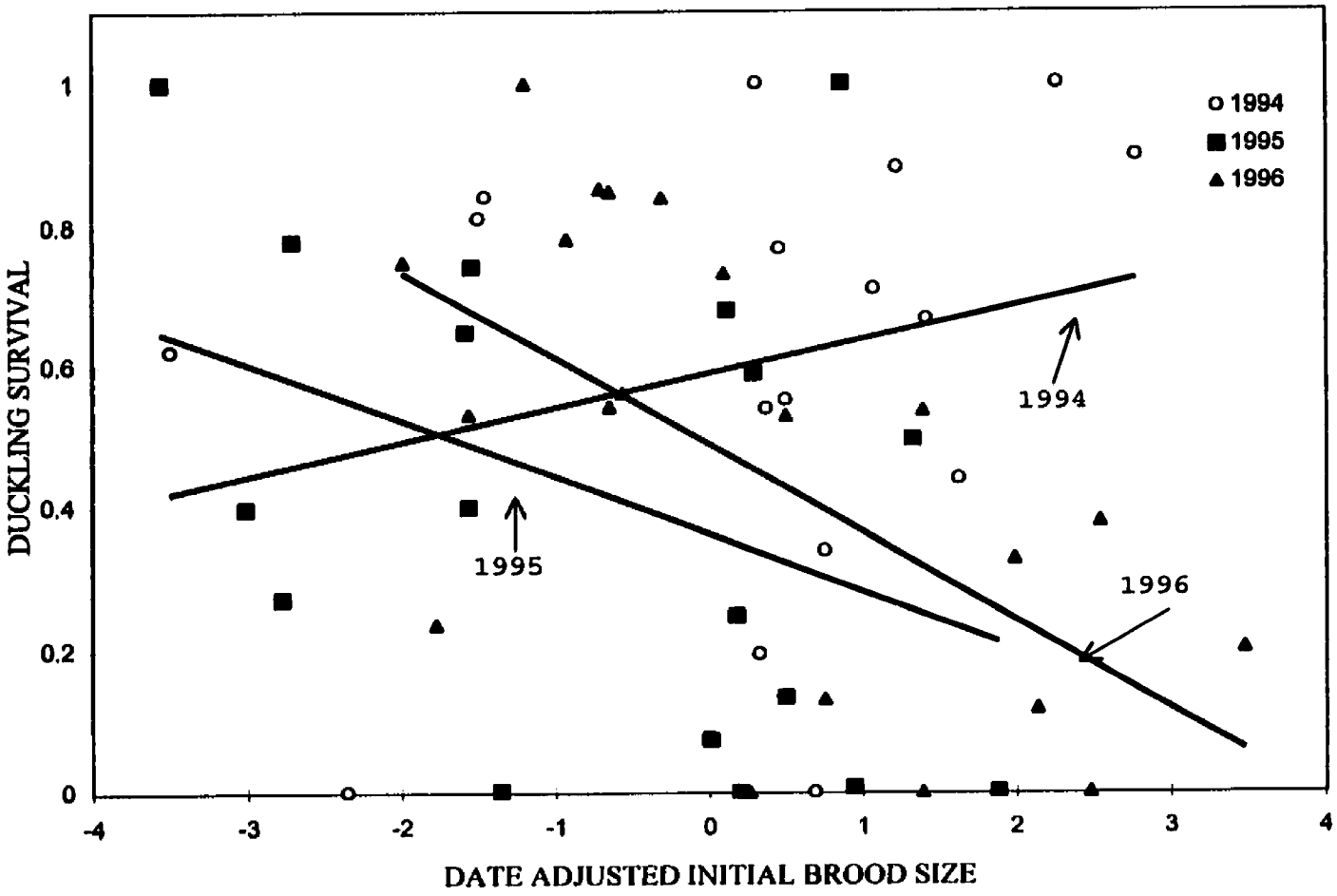

Figure 5.4. Northern Pintail duckling survival in relation to initial brood size at hatch (corrected for hatch date), 1994 - 1996, Kitsim Alberta.

often reported for Mallards (*Anas platyrhynchos*) (Rotella and Ratti 1992a, Mauser et al. 1994). Nonetheless, pintail brood and duckling survival estimates for Kitsim were much greater than those recently reported for pintails in Alaska (3.3 to 14.5%; Grand and Flint 1996b). These findings indicate that there may be substantial temporal and spatial/geographic variation in survival.

I speculate that water conditions are at least partially responsible for the tendency for higher duckling survival in 1994. In 1994, water from the main reservoir was diverted into wetlands during late April, resulting in relatively stable and high wetland water levels throughout most of the brood-rearing period. This additional water, along with favorable precipitation that summer (May/June rainfall; 1994 = 141 mm, 1995 = 89 mm, 1996 = 80 mm; K. Guyn, unpubl. data), kept most wetlands full. Conversely, in 1995 and 1996, many wetlands were drawn down, resulting in several completely dry basins. For example, in 1996, 68% of wetlands in the eastern half of the main study area were either dry or very shallow (i.e., wide mud flats) by early July (K. Guyn, unpubl. data). Finally, Mauser et al. (1994) studied Mallard duckling survival on managed wetlands in California and found that duckling survival was reduced in a year when water was removed from seasonal wetlands prior to peak hatch. In two other years when seasonal wetlands contained water throughout most of the brood-rearing season, survival was higher. My study and that of Mauser et al., further illustrate that duckling survival varies with wetland conditions

5.5.2 Factors Related to Survival

I found that pintail brood and duckling survival decreased with hatching date. In birds, young hatched early in the season often have higher survival to fledging than late hatched offspring (Dow and Fredga 1984, Cooke et al. 1995). In waterfowl, several studies report greater survival to independence for ducklings hatching earlier in the season (Rotella and Ratti 1992a, Grand and Flint 1996b, Dzus and Clark 1998), although this pattern is not consistent (Dawson and Clark 1996).

Several hypotheses have been proposed to explain a seasonal decline in duckling survival. Grand and Flint (1996b) suggested that the late-season decrease in duckling survival of arctic-nesting pintails was related to increased predation on ducklings, mediated by declining availability of alternate prey. In prairie habitats, higher survival of early-hatched ducklings may be related to seasonal declines in wetland quality, as indexed by abundance and depth (Rotella and Ratti 1992b, Dzus and Clark 1998). Although water levels are managed on Kitsim, by mid to late-June many wetlands have reduced water levels, occurring either naturally or due to planned drawdowns. Rotella and Ratti (1992a) found that late-hatched broods in areas of high wetland density also had poor survival, prompting them to suggest that other factors such as reduced invertebrates or increased predator numbers may be responsible. Cox et al. (1998) reported that growth of Mallard ducklings to 17 days was positively related to invertebrate numbers. How invertebrate abundance varied seasonally in Kitsim wetlands and what potential impact this had on pintail duckling survival are unknown. Alternatively, wetlands which are drawn down may increase

in salinity and high salinity concentrations have been found to be fatal to young ducklings (Mitcham and Wobeser 1988).

I did not find strong evidence that ducklings which hatched from nests closer to wetlands had higher survival. Several researchers have suggested that young ducklings are most vulnerable to mortality during overland movement (Ball et al. 1975). Rotella and Ratti (1992a) found that Mallard duckling survival was negatively correlated with distance traveled. However, Talent et al. (1983) and Dzus and Clark (1997a) did not detect a relationship between distance moved and offspring survival.

Duckling survival was associated with a year-by-brood size interaction. In 1994, duckling survival was higher for larger initial broods. This trend was reversed in 1995 and 1996, and perhaps these patterns are related to different yearly habitat conditions. In 1994, flooded vegetation was abundant and this may have afforded protection to large broods, whereas in 1995 and 1996, flooded emergent vegetation was less available and large broods may have been more conspicuous to potential predators. Dzus and Clark (1997b) found that experimentally enlarged Mallard broods showed lower survival to 30 days than did control broods, but total brood loss to 14 days did not differ between enlarged and control broods. Among successful Snow Goose (*Chen caerulescens*) broods, Cooke et al. (1995) found that goslings from small broods tended to have a higher probability of survival, although small broods had higher total brood loss than larger ones. In two of three years I found evidence of a survival advantage for small brood sizes at hatch. Because

pintails have one of the smallest clutch sizes of all dabbling duck species, selection for small brood sizes may at least partially explain this trait. However, experimental manipulation of brood size is required to adequately test this hypothesis.

I found that duckling survival on Kitsim was higher than that reported for pintails in Alaska and similar or higher to estimates for Mallards on the prairies. Early hatched young tended to survive better, and I did not detect any stabilizing selection on timing of nesting. Although Kitsim is a managed wetland project, habitat conditions influenced not only female success (brood survival), but duckling survival, as evidenced by the yearly and annual variation in duckling survival in relation to brood size.

CHAPTER 6. SYNTHESIS

This research focused on a sequence of breeding-season decisions made by Northern Pintails in southern Alberta. Specifically, my research revolved around major decisions and potential tradeoffs relating to nutrient reserve use, nest-site selection, nesting effort and brood rearing. As Beletsky and Orians (1996) point out, the study of breeding season decisions can be viewed from different perspectives. Decisions can viewed relative to variation to lifetime reproductive success or they can be viewed from an environmental perspective. Because almost all decisions are influenced to some degree by variation and predictability of environmental information, I examined breeding season decisions in an environmental context.

Pintails typically inhabit areas with compressed breeding seasons and highly variable environments. Perhaps due to these environmental pressures, pintails tend to nest earlier than most other ducks. In Chapter 2, I examined nutrient reserve use during egg formation in pintails. As reported for pintails in Alaska (Mann and Sedinger 1993, Esler and Grand 1994b), I found that pintails relied on fat reserves during clutch formation more than any other duck species studied to date. Prior to this work, it was unclear whether reliance on fat reserves during clutch formation was an artifact of breeding in the Arctic or a phylogenetic trait. These results indicate that pintails breeding in prairie habitats also rely extensively on fat reserves during egg laying (at least for early-season clutches) and therefore this pattern of fat

reserve use appears species-specific. The pintail's high reliance on lipid reserves during clutch formation may enable them to nest early, a potential advantage in habitats with relatively short nesting seasons. However, further work is needed to fully understand why pintails rely so heavily on fat reserves during clutch formation, and whether nutrient stores are acquired locally or are borne to breeding grounds from elsewhere.

I further examined if there was any evidence that pintails were withholding nutrients for later use. I conducted an interspecific comparison with six other dabbling duck species and found that pintails had the least amount of fat left at the end of laying and invested the least amount of fat into a full clutch. The fact that pintails have little fat left at the end of laying may help to explain why pintails have relatively small clutch sizes and lay few replacement clutches. In Chapter 4, I found that most pintails attempted to renest if their previous nest was lost early in incubation. However, rarely did a pintail nest more than twice, a stark contrast to other species such as mallards. Furthermore, I found a tradeoff between total clutch volume and the interval between nesting attempts; females which made the greatest investments in eggs, also had the longest renesting intervals. Over-investments in initial clutches may have important fitness consequences since, in Chapter 5, I report that duckling survival was reduced for broods hatching later in the season. To my knowledge, this relationship has not been evaluated in other duck species, but such research would be extremely informative.

Similar to other studies (Duncan 1987a, Flint and Grand 1996a), I found that pintails lay relatively small clutches. There is conflicting evidence if and/or which nutrient might limit clutch size in pintails (Mann and Sedinger 1993, Esler and Grand 1994b). In Chapter 2, I did not find any evidence that nutrient reserves limit clutch size in pintails; however, this conclusion was based on a relatively small sample. Thus, further work is needed to resolve this question.

Pintails nesting in the southern prairie face widely differing temperature regimes during the breeding season. They begin nesting in April when temperatures are relatively cool, but the nesting season extends into early July when mid-day ambient temperatures often exceed 30 °C. Since amelioration of nest microclimate may be an important consideration in nest-site choices by birds (e.g., Walsberg 1985), I examined microclimatic conditions at pintail nest-sites in Chapter 3. I tested whether pintails selected nest-sites based on microclimatic conditions and found that nest-sites were cooler (about 2 °C on average) than associated random sites during daylight hours. Furthermore, I found that the temperature difference between nest sites and random sites was greater (nest sites cooler) for nests initiated later in the season, indicating seasonal nest-site selection. Although I did find microclimatic differences between nest and random sites, it is unclear how nest microclimate may affect nutrient allocation decisions. This may be particularly important to pintails, which, as I reported in Chapter 2, appear to have little fat left at the end of laying.

The temperature range for optimum development of a bird's egg is narrow. Although eggs can survive some amount of cooling, they have little tolerance for

extreme heat (Drent 1975). I examined the frequency in which nest-sites and random sites exceeded temperature thresholds and found that the probability of nest-sites reaching lethal temperatures was less than the probability of random sites exceeding this threshold. Some birds have been found to use incubation as a means of cooling eggs and future work exploring incubation rhythms of pintails may indicate if pintail incubation rhythms are timed to protect eggs from extreme heat.

Many of the results from this research indicate that the life history traits of pintails seem particularly well suited for the southern prairie and high arctic; habitats where they typically breed. Both habitats are characterized by short breeding seasons and variable climatic conditions, thereby placing timing constraints on breeding. Unfortunately, some of these traits may also be partly responsible for their decline. The tendency for prairie nesting pintails to nest early and in sparse cover, presumably gives them a great advantage in a habitat that often has few wetlands by mid summer and is characterized by short grass. Regrettably, this trait often leads them to establish nests in crop stubble early in the spring, only to have their nests destroyed during farming operations. Furthermore, it appears that pintails have not evolved the ability to renest repeatedly. Therefore, the loss of these initial nests, particularly late in incubation, places these birds at a serious fitness disadvantage.

Much of the grassland of prairie Canada has been lost (Samson and Knopf 1994), forcing waterfowl to nest in landscapes dominated by cropland. Until recently, some pintails may have been able to successfully nest in summerfallow,

since these fields often were not worked until later in the summer. With increasing agricultural intensity and continuous cropping, even this "habitat" has been decreasing. We need to better understand if and how agricultural intensification has affected pintail populations. If that link is established, potential solutions may become clearer.

With the evidence provided through this research and others, we have a better understanding of the ecological limitations of this species. Pintails are not a species that is well adapted to change; therefore their habitat needs will require special attention if we ever hope to sustain or increase their population.

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APPENDIX A. DECOY TRAP BIAS AND EFFECTS OF MARKERS ON REPRODUCTION OF NORTHERN PINTAILS

A.1 Introduction

Although true random samples are difficult to achieve, researchers should strive to obtain samples that are representative of the study population (White and Garrott 1990). Individuals often need to be captured to estimate survival, recruitment and other population parameters, yet if individuals differ in susceptibility to trapping methods they may not be representative of the population. Decoy traps have been widely used to trap waterfowl (Rogers 1964, Anderson et al. 1980, Sharp and Lokemoen 1987, Dwyer and Baldassarre 1994), but trap bias has rarely been examined. Likewise, researchers often radio-mark animals with the implicit assumptions that (1) radio-marked individuals are representative of the population, and (2) transmitters do not alter behavior or other measures of interest (White and Garrott 1990). In this paper, I quantify possible trap bias, and combined effects of capture and radio-marking, on reproduction of female Northern Pintails (*Anas acuta*; hereafter pintail).

Radio telemetry has been frequently utilized in waterfowl research (e.g., Ball et al. 1975, Gilmer et al. 1977, Ringelman and Longcore 1982, Cowardin et al. 1985, Grand and Flint 1996a,b, Cox and Afton 1997). However, transmitters may have negative effects on birds (e.g., Small and Rusch 1985, Wanless et al. 1988, Paton et

al. 1991), including waterfowl (Sorenson 1989, Pietz et al. 1993, Rotella et al. 1993, Paquette et al. 1997). Back-mounted transmitters attached with harnesses (Dwyer 1972) have been commonly used in waterfowl telemetry studies, but recent evidence suggests that this method may delay nesting (Pietz et al. 1993), decrease nesting effort (Rotella et al. 1993), and reduce survival (Dzus and Clark 1996). Back-mounted transmitters attached with a subcutaneous prong (anchored backpacks) (Mauser and Jarvis 1991, Pietz et al. 1995) and abdominal implants (Korschgen et al. 1984, Olsen et al. 1992) have been suggested as possible alternatives (Rotella et al. 1993, Pietz et al. 1995). Recently, Paquette et al. (1997) compared reproductive effort of Mallards (*Anas platyrhynchos*) with anchored backpacks and abdominal implants; females with anchored backpacks devoted less time to egg laying and incubation, and initiated fewer nests.

Researchers who attempt to evaluate transmitter or marker effects often ignore the possibility that observed effects may result from a combination of trapping and marking. Cox and Afton (1998) reported that female pintails were 16 times more likely to die in the first 4 days after capture and suggested that this mortality was at least partially explained by capture myopathy. Capture myopathy results in degeneration of muscle tissue and can result from intense muscular exertion or trauma associated with restraint (Dabbert and Powell 1993).

Recent literature (Pietz 1993, Paquette et al. 1997) has focused on transmitter effects in Mallards (except Garrettson and Rohwer 1996, Korschgen et al. 1996, Zimmer 1997), but effects may differ with other species of waterfowl, particularly since most are smaller than Mallards. During 1994 - 1996, I studied breeding

ecology of pintails in southern Alberta, using decoy traps to capture females early in the spring. The objective of decoy trapping was to obtain a representative sample of female pintails utilizing the Kitsim project. All decoy trapped females were equipped with anchored backpacks for a study of pintail reproductive ecology. Because I also searched for nests of unmarked birds and captured some of these females on their nests, I had an opportunity to determine whether: (1) decoy-trapped and nest-trapped females had similar body sizes and age distributions (because these would not change after radio-marking); and (2) decoy-trapping, nasal-tagging, and radio-marking (in combination) (hereafter referred to as "radio-marked") affected timing of nesting or reproductive investment.

A.2 Study Area and Methods

During 1994 - 1996, I obtained data from a 40-km^2 study area situated on the Kitsim Ducks Unlimited Project located near Brooks, Alberta ($50^0$30'N, $112^0$3'W). Kitsim contains a main reservoir and 65 managed wetland basins. Basins are interconnected through a canal system that allows irrigation water to flow into them through the main reservoir. Depending on water availability, the basins are usually reflooded in mid-spring and late fall and some become dry by mid-summer. Female pintails were decoy-trapped (Sharp and Lokemoen 1987) during April; with trapping commencing as soon as ponds or pond edges were ice free. Traps were placed on wetlands where pintail pairs frequently were seen. To avoid capturing migrants I did not place traps on wetlands with large flocks of birds. Traps were checked every morning beginning at 0700 and again in the evening starting at 1700. Therefore, 14 hours was the maximum time a female could be in a decoy trap. An

8-g anchored backpack (Advanced Telemetry Systems, Isanti, Minnesota) was attached to each female using a subcutaneous stainless steel wire (anchor), and three subcutaneous sutures (Mauser and Jarvis 1991, Pietz et al. 1995) under local anesthesia. I also attached a standard U.S. Fish and Wildlife Service leg band and nylon nasal tags (Lokemoen and Sharp 1985). Mass (nearest 10 g with a Pesola spring scale), wing chord (nearest 1 mm with a ruler) and head-bill length (nearest 0.1 mm with dial calipers) were measured for all females. The fifth secondary covert was collected and a visual classification of the middle secondary coverts (1995 and 1996 only) was recorded to classify females as second year (SY) or after second year (ASY) following Duncan (1985). After a female was removed from a trap, estimated average handling time from capture to release was approximately ½ hour, with handling time ranging from as short as 20 minutes up to approximately 1 hour. All procedures were approved by the University of Saskatchewan Animal Care Committee (Protocol # 940149) on behalf of the Canadian Council of Animal Care.

I used two nest-searching techniques to acquire information on nests of radio-marked and unmarked females. Nests of most radio-marked females were found by telemetry. Radio-marked females were located twice daily between 0700 and 1300 h from the morning following marking until late July. A female's position was determined by triangulating from two locations using a vehicle-mounted null-array antennae system (4- or 5- element Yagi antennas: Kenward 1987). If a female was located in the same upland location for five consecutive mornings, I approached on foot with a hand-held receiving antenna to determine if she was in nesting cover

and, if she was, she was flushed and I searched for her nest. When a female's nest was found, she was located daily via telemetry to verify her presence at the nest. If the nest was found during egg-laying, I revisited the nest early in incubation to determine full clutch size and to measure the eggs. Once full clutch size was determined, the nest was not revisited until termination (i.e., hatched or destroyed). Nests of unmarked females were located using an 80-m chain dragged between two ATVs (Klett et al. 1986). Nest searches began in early May, when decoy trapping had finished. I attempted to trap all upland nesting females that were still active in late incubation. I used mist nets (Bacon and Evrard 1990), Weller traps (Weller 1957), or walk-in traps (Dietz et al. 1994), and information on female size and age was obtained (as above). I failed to trap 7.6% of upland nesting females that I attempted to capture.

Each time a nest was visited eggs were counted and candled to determine incubation stage; this information was used to estimate clutch-initiation dates (Weller 1956). Full clutch size was recorded as the maximum number of pintail eggs in completed clutches. Length and width of each egg was measured with dial calipers to the nearest 0.1 mm, and egg volume was calculated with the formula of Flint and Grand (1996):

$$\text{Volume} = -0.63392 + 0.53163(\text{length})(\text{width})^2$$

If the eggs hatched, I determined initial brood size by subtracting the number of eggs that did not hatch from the last recorded clutch size.

To check for possible age-specific trap bias, the age structure of females caught in decoy traps was compared to that of nest-trapped females using a chi-square test.

A size index for each trapped female was calculated by summing wing chord and combined length of head-bill. Sizes of decoy-trapped and nest-trapped females were contrasted using analysis of variance (ANOVA), accounting for yearly variation (1994-1996).

To test for combined effects of trapping and marking (radio and nasal marker) on nest-initiation date, ANOVA was performed with PROC GLM (SAS Inst. 1996), first testing for year effects (1994-1996). Because females with anchored backpacks have been reported to renest less frequently than females with abdominal transmitters (Paquette et al. 1997), it is possible that females with anchored backpacks renest less frequently than unmarked females. Therefore, I also re-examined effects on initiation dates by restricting the analysis to nests initiated on or before 18 May. Median nest initiation date of unmarked females was 18 May (n = 244, K. Guyn, unpubl. data). Therefore, nests initiated prior to this date are likely first nests.

To test for combined effects of trapping and marking (radio and nasal marker) on clutch size, I used analysis of covariance (ANCOVA), with year and status (i.e, marked versus not marked) as main effects and initiation date as a covariate. I tested that the homogeneity of slope assumption of ANCOVA was met before proceeding. Since clutch size was not normally distributed the data were $\log_{(10)}$ transformed. Since clutch size in pintails is affected by whether the nest is the bird's first nest or a renest (Duncan 1987, Grand and Flint 1996a), I conducted the same analysis using only first nests (see above). To test for transmitter effects on individual egg lengths, widths, and volumes I used nested ANOVA to account for non-independence of egg

size within a clutch. The number of ducklings hatched between radio-marked and unmarked females was contrasted using ANCOVA with nest-initiation date as the covariate.

Power analyses were performed using the program NCSS Power Analysis and Sample Size (Hintze 1991).

A.3 Results

During 1994 - 1996 I caught 73 female and 806 male pintails in decoy traps. The proportion of SY and ASY females caught in decoy traps versus nest traps did not differ ($\chi^2 = 0.012$; $P = 0.91$; $n = 176$: decoy-trapped; SY = 23, ASY = 47: nest-trapped; SY = 34, ASY = 72).

Size of trapped birds did not differ among years ($F_{2,178} = 0.29$; df; $P = 0.75$) or by capture method ($F_{1,179} = 0.13$; $P = 0.71$; power = 0.99 for a 2% [7 mm] difference in size at $\alpha = 0.05$) (Table A.1). When all nests were included, nest-initiation dates differed among years ($F_{2,291} = 6.62$; $P = 0.002$), therefore, analyses were conducted for each year. Nest-initiation dates did not differ between radio-marked (decoy-trapped) and unmarked females in 1994 ($F_{1,86} = 0.21$; $P = 0.65$; power = 0.24 for a 5% difference [6.6 days] in initiation date at $\alpha = 0.05$) or 1995 ($F_{1,92} = 0.58$; $P = 0.45$; power = 0.38 for a 5% difference [6.7 days] in initiation date at $\alpha = 0.05$). In 1996, average nest initiation date for radio-marked birds tended to be earlier than that of unmarked females ($F_{1,113} = 3.68$; $P = 0.06$) (Table A.1). When only first nests were included (see above) clutch-initiation dates did not vary among years ($F_{2,158} = 0.37$; $P = 0.69$) nor between radio-marked and unmarked females ($F_{1,159} = 1.40$; $P = 0.24$; power = 0.86 for a 5% [6 day] difference in clutch

Table A.1. Size and nesting data for radio-marked and unmarked female Pintails at Kitsim, Alberta, 1994 - 1996.

	Unmarked[b]			Radio-marked[c]		
	$\bar{x}$	(SE)	n	$\bar{x}$	(SE)	n
Size[a]	352.8	(0.67)	108	353.6	(0.82)	71
Clutch Initiation Date						
94	132	(2.0)	74	135	(4.4)	13
95	134	(2.1)	68	137	(2.8)	25
96	142	(1.7)	102	132	(4.8)	12
First Nest	122	(0.9)	130	125	(1.6)	30
Clutch Size[de]	7.08	(1.3)	115	6.86	(1.2)	36
Egg Volume	39.6	(0.26)	74	39.2	(0.52)	23
Ducklings Hatched[e]	6.5	(0.31)	31	6.5	(0.46)	15

[a] size = wing + head-bill length
[b] includes females nest-trapped late in incubation
[c] decoy-trapped in early spring
[d] date corrected
[e] upland nests only

initiation date at $\alpha = 0.05$). Of the decoy trapped pintails that I was able to monitor closely ($n = 56$ birds that stayed on the study site), 73% initiated nests, but I have no way of assessing whether my estimate of non-breeding (27%) is reliable.

Clutch size did not vary among years ($F_{2,215} = 0.30$; $P = 0.58$) but when all pintail nests were included, radio-marked birds produced smaller clutches than unmarked females ($F_{1,216} = 3.83$; $P = 0.05$). Some nests of unmarked females ($n = 66$) were located on islands and, since many nests on islands were parasitized (K. Guyn, unpubl. data), full clutch sizes may have been biased high if parasitic eggs went undetected. To account for this, I restricted analyses to upland nests and found only a weak trend for radio-marked females to lay fewer eggs ($F_{1,150} = 2.82$; $P = 0.09$) (Table A.1). When I restricted the analysis to first nests, full clutch sizes did not differ between radio-marked and unmarked females ($F_{1,114} = 0.95$; $P = 0.33$). Individual egg volumes ($F_{1,104} = 0.63$; $P = 0.43$), lengths ($F_{1,104} = 0.23$, $P = 0.63$) and widths ($F_{1,104} = 2.71$; $P = 0.10$) did not vary between marked and unmarked females. Period from capture to nest initiation for radio-marked females averaged 19.3, 24.8 and 19.5 days in 1994 – 1996, respectively; with no difference between years ($F_{2,33} = 1.18$; $P = 0.31$). Number of ducklings hatched from upland nests (corrected for date) did not differ between marked and unmarked females ($F_{1,46} = 0.01$; $P = 0.93$; power = 0.20 for a 10% [0.65] difference in number of ducklings hatched at $\alpha = 0.05$).

A.4 Discussion

Despite the relatively common use of decoy traps to capture waterfowl, few studies acknowledge or investigate potential trap biases. Weatherhead and Greenwood (1981) suggested that Red-winged Blackbirds (*Agelaius phoeniceus*)

captured in decoy traps were in poor condition and not representative of the population. Grand and Fondell (1994) reported that fewer older female pintails were captured in decoy traps than with rocket nets. They suggested that ASY females were either less aggressive towards unfamiliar females, more wary of decoy traps or were already incubating when they were decoy trapping. I found no difference in the age distribution or size of decoy-trapped versus nest-trapped female pintails.

Although I detected no age or size-specific effects of decoy traps, other factors should be considered before choosing this capture method. For instance, female pintails were relatively difficult to capture. I trapped 73 female pintails, but incidentally caught 161 female mallards and 806 male pintails (K. Guyn, unpubl. data). Female pintails may be more wary or less aggressive than male pintails or female mallards, making them more difficult to capture in decoy traps. I captured > 10 males (not including recaptures) for every female. Male pintails are known to have weak pair-bonds, take part in extra-pair copulations and exhibit extra-pair chase behavior (Smith 1968). Grand and Fondell (1994) suggested these behavioral traits may make males susceptible to capture in decoy traps.

I likely misclassified the age of some females (Esler and Grand 1994a). However, the proportion of SY to ASY females was nearly identical for decoy and nest-trapped birds, so it is unlikely that misclassification led to incorrect conclusions regarding trap bias. Given that my sample of unmarked females is derived from females nest-trapped late in incubation and that older females can be more successful breeders (Afton 1984, Dow and Fredga 1984), my sample of unmarked

birds may be biased. However, since I did not detect age or size differences between females caught in decoy-traps and caught on nests, this would suggest that both samples are biased in the same direction. This is unlikely, since results from previous workers suggest that young females were more susceptible to decoy traps (Grand and Fondell 1994). Nonetheless, some caution should be taken when interpreting my results because decoy-trapped and nest-trapped birds may have differed in ways I did not assess.

Potential deleterious effects of harness-style transmitter attachments on reproduction have recently been reported (Pietz et al. 1993, Rotella et al. 1993), and many researchers have turned to anchored backpacks and abdominal implants as alternatives. I could not conduct a clear evaluation of radio transmitter effects alone with pintails, because all radio-marked females were also nasal-tagged and decoy-trapped. In 1996, clutch initiation dates differed between radio-marked and unmarked females, and upon closer examination it appears that radio-marked females did not nest as frequently later in the season. Furthermore, analysis of clutch-initiation date in 1994 and 1995 had modest power, so it would be unwise to conclude that there was no effect. Female pintails with anchored backpacks did not differ from unmarked females in first clutch initiation dates, but radio-marked birds did have reduced clutch size. However, the biological significance of a 0.22 difference in clutch size is questionable. Paquette et al. (1997) compared Mallards with abdominal implants and anchored backpacks and found no difference in median initiation of first nests, size of first clutch, or proportion of females that

nested. However, females with anchored backpacks devoted less time to egg laying and incubation and initiated fewer nests.

If capture/handling did influence female behavior, it is likely related to increased risk of abandoning nests already initiated at the time of capture or a delay in nest initiation. If trapping birds resulted in abandonment of active nests, then some first nests found for radio-marked birds would have actually been renests. Since renests tend to have smaller clutches than first nests (Duncan 1987, Grand and Flint 1996) this could result in lower average clutch size for radio-marked birds. Similarly if trapping resulted in nest abandonment or a delay in nest initiation, average nest initiation dates for radio-marked females would be later. However, I found no evidence that radio-marked females delayed nest initiation.

Mallards equipped with harness-style backpacks spent less time feeding than unmarked Mallards (Pietz et al. 1993), and this could be responsible for reduced reproductive effort in radio-marked Mallards. Although I did not conduct behavior observations, several radio-marked pintails were seen pulling on their transmitters (K. Guyn, pers. obs.). Decoy trapped female mallards with similar back-mounted transmitters were found to have lower brood survival than abdominally implanted females (J. Devries, pers. com.). They speculated that partial detachment of the back-mounted design resulted in irritation leading to reduced vigilance.

All radio-marked pintails were also nasal-tagged. Howerter et al. (1997) compared nasal-tagged and unmarked Mallards and found that although nasal-marked females tended to initiate their first nest 2 – 6 days later, there was no difference in the proportion that nested, number of nest attempts or nest success.

They suggested that because there was only a small difference between the two groups that nasal tags not be abandoned as a marking technique. I did not find that decoy- trapped females marked with nasal tags and radios nested later than unmarked controls.

To conclude, I did not detect a trap bias with decoy traps, but pintails were difficult to capture and the method was very time and labor intensive. My results suggest that combined effects of trapping and marking may negatively affect some aspects of reproduction in pintails. I suggest that if implants are not an alternative, the use of anchored backpacks should be carefully considered in light of study objectives.